

The University of Chicago

**A STUDY OF THE CRYPTOZOA OF AN
ILLINOIS WOODLAND**

A DISSERTATION SUBMITTED TO THE FACULTY OF THE
DIVISION OF THE BIOLOGICAL SCIENCES IN CANDIDACY
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOÖLOGY
1944

By
LAMONT C. COLE

Reprinted from
ECOLOGICAL MONOGRAPHS
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A STUDY OF THE CRYPTOZOA OF AN ILLINOIS WOODLAND

INTRODUCTION

The term "cryptozoic fauna" was coined by Dendy (1895) to describe "the assemblage of small terrestrial animals found dwelling in darkness beneath stones, rotten logs, the bark of trees, and in other similar situations." This term, or the less redundant form "cryptozoa," has never attained wide usage and has sometimes been extended, for example by Willey (1911) and Grimmet (1926), to include "all animals that avoid the light of day; crepuscular, nocturnal, and subterranean forms."

Dendy considers the cryptozoic fauna to be a unit as distinct as the littoral or abyssal faunas of the ocean and passing as gradually into other faunas, in this case the soil or hypogeous fauna and the vast assemblage of animals living in open daylight.

From October 1941 through December 1943 the writer studied, with as little disturbance as possible, animals which collected under boards of uniform size placed on the forest floor. These animals were clearly cryptozoa plus an assortment of stragglers from other niches. They were, however, only a portion, perhaps a hypogenous aspect, of the cryptozoic fauna as defined by Dendy because a somewhat different assemblage of species is to be found in rotten logs and beneath the bark of trees.

The typical inhabitants of the cryptozoic niche are refugees from physical conditions or from biotic factors of predation or competition in the outside environment. Five general categories of animals, four of which were distinguished by Dendy, are recognizable within the cryptozoic fauna. There are: relict forms, forms in transition from aquatic to terrestrial life, larvae or other immature stages, seasonal residents which hibernate or reproduce in the cryptozoic niche, and an assortment of representatives of modern, dominant, terrestrial groups which are either specially adapted to this niche or are less capable of succeeding in more rigorous environments.

The relict cryptozoa, unrepresented in this study unless the pseudoscorpions be listed, are exemplified by the Onychophora, and the category also includes scorpions and other members of ancient and subsiding animal groups.

The incompletely modified aquatic forms include terrestrial turbellarians and nemerteans, and especially the very characteristic terrestrial crustaceans, particularly isopods of the suborder Oniseoidea. These are uniformly very sensitive to drying and frequently to freezing and they are mostly poorly adapted for digging. The cryptozoic niche provides shelter, a suitable food supply, and avenues for migration into the soil, and hence is an ideal habitat for these forms.

The immature and seasonal forms are chiefly insects, larvae of species in which the adults may or may not be cryptozoic, ovipositing adults of species having cryptozoic larvae, and hibernating adult insects which spend most of their lives in other niches.

Modern successful groups are represented among the cryptozoa principally by slugs, snails, spiders, centipedes, diplopods, and insects. Dendy mentions the roaches, beetles, and ants as the most characteristic insects although it seems that we should add to these the collembola and perhaps the earwigs.

It would be premature from the evidence to be presented to call these animals a fauna in the sense understood by Jacot (1940) and others if the term must signify a taxonomic assemblage of species devoid of integration. The writer is, however, reluctant to speak of studying an animal community, society, or a biocenosis as these concepts frequently imply an integrated unit at the organismic or supra-organismic level (see Beklemishev quoted by Carpenter 1939). Hence, in this paper the term "cryptozoic fauna" will be used in the geographic sense to describe a regional assemblage of cryptozoa and without implications as to interrelationships between the constituent species.

Since the 1895 account by Dendy there seem to have been no studies dealing specifically and exclusively with the cryptozoa of any region although some workers (e.g., Hayes 1927) seem to have recognized the existence of a distinctive fauna in this niche. There have, however, been numerous studies of the fauna of the soil (for extended bibliographies see Waksman 1932 and Jacot 1940) and of the fauna of the forest litter (see especially Bornebusch 1930). Both of these overlap the cryptozoic fauna to a considerable extent and, since debris such as fallen timber is often included in the samples, much information on the cryptozoic fauna may be obtained from such accounts. Many of these accounts (Diem 1903, Dammerman 1925) mention that certain forms are more typically found under stones and logs than in the mineral soil or litter. In some general ecological surveys, such as that of Anderson & Falk (1935) on the central desert of Iceland, a large proportion of the invertebrate fauna has been obtained from beneath stones. Other general ecological studies such as those of Adams (1915a), Weese (1924), and Blake (1926) mention particular forms typically found under logs and stones, and it is also possible to obtain information on the cryptozoa of a region from faunal lists such as that of Lindroth (1931) which include accounts of the habitats in which forms are found. Such reviews leave one impressed by the uniformity of the fauna of this habitat wherever it has been investigated. Certain taxonomic groups, often as narrow as families or genera, seem to pre-

dominate in the cryptozoic fauna over most of the earth while other groups are typical of tropical or temperate cryptozoic faunas in both the old and new worlds.

This paper is a revision of a Ph.D. thesis submitted to the Department of Zoology of the University of Chicago in the spring of 1944. This revision has been considerably retarded by the writer's call to active duty with the United States Public Health Service soon following convocation. Much gratitude is due to Dr. Thomas Park who directed this research. The writer is also indebted in numerous ways to Dr. W. C. Allee, Dr. Alfred E. Emerson, and Dr. Sewall Wright. Thanks are also due Professor C. R. Smith of Aurora College for providing daily weather records, to Dr. and Mrs. F. C. Cole for the use of their property, to Mrs. Lamont C. Cole for assistance in various ways, and to the following specialists for the identification of specimens: Dr. Fritz Haas (Molluses and Isopods), Dr. Harlow B. Mills, (Collembola), Dr. R. V. Chamberlin (Chilopods and Diplopods), Dr. H. E. Ewing (Acarina), Dr. Donald C. Lowrie (Spiders), Mr. J. A. G. Rehn (certain Orthoptera), Mr. W. M. Gerhardt (Hemiptera), Mr. Rupert Wenzel and Mr. Henry Dybas (Coleoptera except Staphylinidae), Dr. Charles Seevers (Staphylinidae), and Dr. Mary Talbot (Ants).

THE LOCALITY STUDIED

This study was conducted within a woodland having an area of approximately 40 acres located on a 173-acre farm 2.5 miles north of the town of Plano in Kendall County, Illinois. The trees in this woodland are largely black oak (*Quercus velutina*), bur oak (*Q. macrocarpa*), and shagbark hickory (*Carya ovata*) although other species, notably slippery elm (*Ulmus fulva*), were present up until about 1933. These woods have been grazed by cattle for many years and are largely devoid of underbrush and second growth except for one small portion which has been fenced and protected from grazing since 1935. In this ungrazed area there is a considerable growth of underbrush consisting largely of black cherry (*Prunus serotina*), raspberry (*Rubus* sp.), and oak and hickory seedlings. A few elms (*Ulmus americana*) and sugar maples (*Acer saccharum*) have been planted in the enclosure. The soil in the grazed portion of the woods is for the most part covered with a thick growth of grass.

A small perennial stream emptying into Little Rock Creek about one-half mile distant, traverses this woodland which was once continuous with the woods bordering Little Rock Creek but which was isolated many years ago through the cutting of trees on adjacent farms.

Two localities, both located at a level about 6 meters above that of the small stream, were utilized. One of the localities (hereafter referred to as locality G) was situated in a thinly forested and heavily grazed portion of the woods which was first fenced to prevent grazing in October 1941, the time at

which this study was started. A number of stumps of oaks which had been cut since 1935 were located in this locality. The other locality (hereafter called locality U, because ungrazed) was last grazed by cattle in 1934 and hence was a region of considerable undergrowth and contained many young trees. The two localities were separated by a distance of approximately 100 meters.

Certain differences in the surface soils of the two localities, probably referable to the effects of grazing, are shown in Table 1.

TABLE 1. Comparison of the surface soil under boards in the grazed (G) and ungrazed (U) portions of the woodland.

Factor	No. of samples each locality	MEAN VALUE AND S.E.		RANGE OF VALUES	
		U	G	U	G
Organic matter (percent).....	5	5.1	3.4	4.9-6.0	2.7-4.4
PH.....	25	6.70±0.34	6.33±0.34	6.2-7.2	6.0-6.7
Hygroscopic coefficient.....	1	11.9	3.8		

Because this study was centered about the surface soil rather than the mineral soil itself, samples for these comparisons were taken from the surface in contact with the undersides of boards lying on the forest floor. Organic matter is very unevenly distributed in this surface layer resulting in much variability among samples and making it practically impossible to use random samples for detecting significant differences between the two localities. Table 1 does suggest, as might be anticipated, that the surface soil of the ungrazed locality was more alkaline, contained more organic matter, and was capable of retaining more moisture than that of the grazed locality.

The hygroscopic coefficient (Miller 1931, Weaver & Clements 1938) is a measure of the amount of moisture which a dry soil will absorb from a saturated atmosphere and which is held so tenaciously as to be unavailable to the roots of plants. This water must, however, be lost from the soil in an unsaturated atmosphere and so must serve to maintain humid conditions in the soil and beneath debris on the surface. In dry weather the humidity must remain higher under boards lying on the soil with the higher hygroscopic coefficient. The total water retaining capacity of a soil varies directly with the hygroscopic coefficient and it will be shown that the soil in the ungrazed portion of the woods actually did retain more water than the soil of locality G.

There were other obvious differences between the environments of the two localities. Air movement was greater in locality G and the autumn and winter covering of leaves was heavier in locality U. The thicker forest canopy in locality U also resulted in increased shade and less variable soil temperatures.

No apparent barriers other than environmental conditions prevented migration of species between

localities U and G. On this same farm, about 1/4 mile from area U, is another small grove of trees growing in a moist depression in the original prairie. The soil in this grove is more continuously moist than in the woods, the trees include cottonwoods (*Populus deltoides*), and the area has not been exposed to either grazing or cultivation. No detailed study was made of the cryptozoa in this grove but casual observations revealed the presence of a number of species not found in the extensive study of the larger woodland. These included the gastropods *Polygyra* spp. (one immature *Polygyra* was taken in the woodland), *Anguispira alternata*, *Philomachus* sp., *Succinea* sp., and the diplopods *Fontaria* sp., *Julus* sp., and *Spirobolus marginatus*. All of these are forms typically found in the more humid beech-maple forests south and east of Chicago. Unfavorable environmental conditions presumably have prevented colonization of the nearby woodland by these species.

METHODS OF STUDY

The unit of observation employed was a board 3.8 cm. thick, 14 cm. wide, and 28.5 cm. long, thus having an area of 400 cm.² in contact with the ground. The boards were cut from well-seasoned oak and were solid enough to provide no entrance for macroscopic animals into the body of the board.

The boards were placed directly on the ground, grouped into "areas" arranged in an attempt to obtain full representation of all types of locations included in the fenced areas. Each board was separated from its neighbors by a distance of at least 1 m. The total number of boards considered in this report is 369 grouped into several areas as shown in Table 2.

TABLE 2. The experimental areas employed. "U" signifies ungrazed locality and "G" signifies grazed portion of woods.

Designation of area	Date established	Number of boards	Location
H.....	11- 1-41	20	U
X.....	6-19-42	15	U
TP.....	3-26-42	121	U
NN.....	9-16-42	15	U
Miscellaneous.....		17	U
A.....	10-22-41	20	G
B.....	10-26-41	40	G
C.....	10-26-41	20	G
D.....	10-26-41	20	G
DD.....	11- 1-41	6	G
O.....	11- 1-41	44	G ¹
Miscellaneous.....		26	G

¹Actually outside of the fenced locality G, placed as a control for the effects of grazing cattle.

There was a total of 193 boards in the ungrazed region U and 176 boards in the grazed region G. Special characteristics of the areas are described below.

DESCRIPTION OF AREAS

Area A. The boards were placed around the periphery of a rectangle about 3 m. by 6 m. in size, the

sod being removed before each board was placed. Ten of the boards, forming the south and west sides of the rectangle, were twice the regular size and consisted of two of the standard boards fastened together along one of the side edges. The grass in this area was continually cut so that it did not exceed a height of approximately 5 cm.

Area B. These boards were placed in four rows about 1.5 m. apart. The sod was not removed but a trowel was used to thoroughly "plow" and loosen the soil to a depth of 15 cm. under the odd-numbered boards only. Every fifth board was double-sized as described above. No faunal differences were detected which could be referred either to the plowing of the soil in this area or to the removal of the sod in Area A.

Area C. This area was laid out in a roughly circular shape in a location which contained a dense growth of tall weeds each year. The soil seemed particularly poor in this area probably as a result of the burning off of a large patch of Canada thistles in 1940.

Area D. These boards were placed in two straight lines of ten each, located 1.5 m. apart. The sod and the upper 5 cm. of soil was removed from beneath each board and replaced by soil brought from the ungrazed portion of the woods. As in Area A, the grass and weeds were kept cut. During part of the study this area and Area H were watered with a sprinkling can.

Area O. These 44 boards were scattered irregularly outside of the fence surrounding the study locality. Owing to disturbance of the boards by grazing cattle, this area yielded very inconsistent results.

Area DD. This area consisted of six boards with six others placed on top of them, the boards being held apart by strips of wood 5 mm. thick.

Miscellaneous boards in the grazed locality. These boards, mostly placed for special experiments, included three "boards" which were in reality iron plates employed to determine the effect of type of sheltering material. They also included three "boards" cut from decaying stumps and consisting of very soft, spongy wood into which animals could penetrate; three "boards" consisting of bark removed from a felled tree; and eight of the standard boards where an unsuccessful attempt was made to isolate them against surface migration by a surrounding galvanized iron barrier extending 13 cm. above the ground and 10 cm. below. The other ten miscellaneous boards were well-weathered cedar shingles placed in order to ascertain the effect of a thinner board offering less protection from heat penetration.

Area H. The twenty boards formed one straight line through a region of thick underbrush where they received very little sunlight. There was almost no grass in this area and decaying leaves were raked aside in order to place the boards.

Area X. These boards were in three rows of five each in a sunny grass-covered portion of the ungrazed locality. The grass in this area was continually kept cut. This area was used chiefly to investi-

gate the effect of temperature on the fauna. Five of the boards retained their natural wood color, five were painted on the upper surface with white enamel, and the remaining five boards were painted a dead black on the upper surface with a mixture of lamp-black and clear varnish. The distribution of the three types of boards within the area was at random and was altered twice during the course of the study as a check on the validity of results. This area received direct sunlight through a large part of each sunny day and under these conditions the temperature under the blackened boards rose from 2° to 4° C. above that of the white or natural-colored boards. The white boards, in the early part of the study, averaged slightly cooler than the natural-colored boards.

Area TP. The 121 boards were arranged in two rows around the eastern and northern sides of the ungrazed locality. This area included all types of cover to be found in this portion of the woods; short grass, tall grass, bare ground, and all degrees of exposure to the sun ranging from continuous exposure to continuous shade under thick bushes.

Area N. These five boards were located in tall grass.

Area NN. This area, which formed a straight line on short grass some 15 m. from any other area, was established at a time when it could be inspected every six hours for one week in order to check the rate at which animals would move into a newly established area.

The *miscellaneous boards* in the ungrazed locality included iron plates, two iron automobile running boards, concrete and tile blocks, and double and triple sized boards.

METHOD OF SAMPLING

The animals under the boards were counted by quickly turning the board up onto one edge and counting all of the animals visible both on the surface of the ground and adhering to the under surface of the board. No attempt was made to discover animals which had migrated vertically into the soil as these were considered to have left the cryptozoic niche and consideration of these emigrants would have seriously disturbed the habitat. With some practice an observer can count all of the individuals of the larger species normally found under a board of this size and the number of species found in such a restricted niche is sufficiently small that an investigator may become well acquainted with them and recognize the majority on sight. The faster-moving species must be counted first and the body of the observer should shade the board when it is turned over as bright light causes the animals to scatter more rapidly. After making the count the board was quickly replaced in its original position and the results recorded. Counts made at four-hour intervals checked very well with each other provided there had been no radical change in the outside conditions. Disturbance of the animals was generally quite noticeable after a one-hour interval and frequently after

two hours because the disturbed animals would enter holes in the ground or run into the grass at the edge of the board and not move back directly beneath the board for some time.

No evidence was obtained to suggest that the fauna was more than temporarily affected by raising the boards to count the animals. The three following considerations suggest that disturbance was without significant influence on the fauna:

1. Control boards which were not inspected for long periods of time, in some cases for an entire year, sheltered the same species as boards which had long been inspected several times weekly. Also, in the relative abundance of the various species, these control boards always fell within the range exhibited by the experimental boards.

2. Whenever study was resumed on an area which had not been inspected for some time, the species which were initially present persisted even under a routine of very frequent inspections. Under such conditions the numbers of animals varied irregularly with time and independently of the time of inspections (see Figs. 5 and 6).

3. As shown in Figure 7, the numbers of animals in different experimental areas tended to vary simultaneously thus indicating response to widespread environmental changes rather than to local accidents of disturbance.

Ants, mites, and collembola could not be accurately counted by the sampling method employed. Ants were counted when not more than about 25 were present under a board and the numbers in larger colonies were merely estimated. These relative figures doubtless reflect real changes in ant abundance but the absolute numbers recorded are not to be taken very seriously. Presence or absence of groups of ants as large as 25 may, however, be used as an exact criterion of ant abundance for statistical purposes. Mites were never abundant under the boards and they were more characteristic of the mineral soil and general litter than of the cryptozoic niche. Ordinarily only presence, absence, or unusual abundance was recorded for mites, nematodes, Corrodentia, and similarly noncharacteristic forms. The most serious fault of the assay method was that it did not yield truly quantitative data on the characteristic and abundant collembola. When a board was turned over some collembola remained attached to the underside and the numbers of these adhering collembola were found to correlate with certain other biotic data. However, this habit of the collembola is probably less related to the actual numbers present than to the presence of an invisible film of moisture. No really satisfactory method of assaying collembola was devised.

Specimens of all of the species encountered were collected, and these have for the most part been identified by experts. Except where absolutely necessary these collections were not made from under experimental boards but were taken from under naturally fallen timber or more frequently from under neighboring boards not used in the quantita-

tive study. When a species was encountered for the first time under an experimental board, the first specimen was collected there and the species designated by an identifying symbol pending accurate identification. Thus an attempt was made to keep disturbance of the natural fauna at a minimum. Data from boards which were obviously disturbed by extraneous factors (usually moles, but occasionally other mammals) were not used for analytical purposes.

Temperature and relative humidity data, and notes on general weather conditions were kept for all days on which boards were inspected. Daily weather reports for the entire period of the study were obtained from Aurora College, the nearest official U. S. weather station, located about 12.6 miles map distance from the site of the study.

Soil and air temperatures, particularly the surface temperature taken by pushing the bulb of the thermometer between the soil surface and the board before raising it, were recorded each time the boards were inspected. Many soil samples of about 15 gms. each were also collected for soil moisture determinations which were made gravimetrically, the soil moisture being expressed as percentage of the 40° C. dry weight. Extensive series of such samples were not collected until the latter part of the study because it was felt that removal of soil might affect the fauna. Moisture determinations of this type do not necessarily reveal typical conditions because the soil under a single board may exhibit considerable local variations in wetness.

In addition to the inspection of boards, other local niches were always examined for animals. Fallen leaves and branches were turned over, digging was done in the sod, and dead stumps and the bark of trees searched. At night the grass and other plants near boards were inspected to determine the amount of nocturnal wandering of the fauna and in winter some digging was done in the ground and in stumps and logs in order to locate the hibernacula of the cryptozoic animals.

LABORATORY STUDIES

Although laboratory study of animals from under the boards was not extensive, many animals were brought alive into the laboratory for observation and some toleration and behavior tests were conducted.

A large covered pan of woodland soil, heavily inoculated with animals from the field, was kept in the laboratory, permitting observation of the animals under a deep red light which did not stop them from feeding and wandering about over the soil surface. Attempts to rear larvae under these conditions were not very successful.

For a check on food habits, the stomach contents of a number of species were examined microscopically.

Most of the important species were tested for their reactions to atmospheric humidity through the use of a humidity gradient apparatus designed on a plan

similar to that described by Williams (1934). By using various salt solutions, the intensity of the gradient of relative humidity could be controlled and a small hygrometer the size of the vials holding the solutions was used to check the humidity in each compartment of the apparatus.

Many species were also tested for their reactions to wet and dry substrata by a method similar to that described by Allee (1926). A piece of porous paper toweling was placed on a glass plate and over this was inverted one-half of a 30-cm. crystallization dish containing the animals to be tested. Water placed on the projecting edge of the paper towel moistened a portion of the paper under the dish by capillary action and the extent of the moistened substratum could easily be detected visually. The whole set-up was left in a darkened room and occasionally inspected under a dull red light to observe the reactions of the animals.

Certain species were also tested for toleration of low temperatures using the freezing chamber of an electric refrigerator, and some aggregations of gregarious forms were tested for possible effects on the rate of heat loss (Allee 1926). Temperature in each case was read from outside by means of a copper-constantan thermocouple.

Other techniques have been discussed in describing the experimental areas. Statistical methods employed in treating the data will be discussed as the data are presented.

THE GENERAL CHARACTER OF THE CRYPTOZOIC FAUNA IN THIS AND IN OTHER STUDIES

So far as could be determined, the fauna investigated in this study was a natural fauna exactly equivalent to that occurring under natural debris lying on the forest floor. During the course of the study many logs, stones, and pieces of bark were inspected for comparison with the experimental boards. As would be anticipated, the fauna under these objects was numerically much more variable than that under the boards owing to variations in size and condition of the debris. However, no species were ever found under natural debris which did not also occur under the boards, and every natural station investigated, in the percentage composition of its fauna, fell within the range displayed by the experimental boards. The fauna investigated, although equivalent to a naturally occurring fauna, was more susceptible to quantitative study because the factors of available shelter and permeability of the wood were controlled.

Somewhat over 130 species of animals were found in the cryptozoic niche. Many of these were encountered so rarely as to be obviously accidental occurrences and many others were demonstrably more abundant in some other niche. Below is a nearly complete list of the forms encountered including not only the truly cryptozoic animals but also forms which occurred under the boards seasonally or acci-

dentially. For analytical purposes the list was abbreviated to include only the more typical cryptozoa which will be considered in greater detail.

LIST OF THE SPECIES ENCOUNTERED

- Platyhelminthes
1. Turbellaria, unidentified species
2. Nematoda, unidentified species
Annelida—Oligochaeta
3. Lumbricidae, unidentified species
Mollusca—Gastropoda—Pulmonata
Limacidae
4. *Deroceas agreste* (L.)
Zonitidae
5. *Retinella rhoadsi* (Pilsbry)
Endodontidae
6. *Helicodiscus parallelus* (Say)
Helicidae
7. *Polygyra* sp.
Arthropoda
Crustacea—Isopoda
8. *Trachelipus rathkei* (Brandt)
Arachnida
9. Chelonethida, unidentified species
Acarina
10. Unidentified spider mite
11. Unidentified larval Erythraeidae
12, 13, 14. Parasitidae, three unidentified spp.
Araneida (most of the spiders were not identified)
Thomisidae
15. *Xisticus gulosus* Keyserling
16. *Tibellus oblongus* (Walekenaer)
17. *Philodromus aureolus* (Oliv.)
18. *Misumenoides aleatorius* (Hentz)
Theridiidae
19. *Steatoda borealis* (Hentz)
Lycosidae
20. *Arctosa littoralis* (Hentz)
21. *Lycosa avida* Walck.
22. *Pardosa milvina* (Hentz)
23. Drassidae, unidentified species
24. Clubionidae, several unidentified spp.
25. Sciaridae, unidentified species
26. Attidae, several unidentified spp.
27. Argiopidae, several unidentified spp.
28. Agelenidae, unidentified species
Phalangida
29. Phalangidae, unidentified species
Chilopoda
Geophilidae
30. *Arenophilus bipuncticeps* (Wood)
Lithobiidae
31. *Lithobius forficatus* (L.)
Diplopoda
Julidae
32. *Aniulus diversifrons* (Wood)
Polydesmidae
33. *Scytonotus granulatus* (Say)
34. *Pseudopolydesmus serratus* (Say)
Hexapoda
Diplura
35. Unidentified dipluran species
Collembola
Sminthuridae
36. *Ptenothrix marmoratus* Packard
Entomobryidae
37. *Entomobrya purpurascens* Packard
38. *Pseudosinella violenta rolfsi* Mills
39. *Tomocerus flavescens* Tib. var. *americanus* Sch.?
40. *Isotoma viridis* Bourlet
Orthoptera
Blattidae
41. *Parcoblatta pennsylvanica* DeGeer
Gryllidae
42. *Gryllus assimilis* v. *pennsylvanicus* Burm.
43. *Nemobius carolinus* So.
Locustidae
44. *Tettigidea lateralis parvipennis* (Harr.)
Tettigoniidae
45. *Ceuthophilus* sp.
Homoptera
46. Cicadellidae, unidentified species
Hemiptera
Coreidae
47. *Leptocomis trivittatus* Say
Lygaeidae
48. *Myodochus serripes* Oliv.
49. *Blissus leucopterus* (Say)
Reduviidae
50. *Melanolestes picipes* Herr.-Sch.
Coleoptera
Cicindelidae
51. *Cicindela sexguttata* Fab.
Carabidae
52. *Abacids* sp.
53. *Euferonia stygia* (Say)
54. *Stenocellus* sp.
55. *Anaferonia* sp.
56. *Dicaelus elongatus* Bon.
57. *Harpalus vulpeculus* Say
58. *H. vagans* Lee.
59. *Platynus placidus* (Say)
60. *P. cupripennis* (Say)
61. *Calathus gregarius* Dej.
62. *Galerita janus* Fab.
63. *Notiophilus aeneus* Hbst.
64. *Casnomia pennsylvanica* L.
65. *Anomoglossus emarginatus* Say
66. *Scirites substriatus* Hald.
67. *Pristodactyla unipunctata* (Say)
68. *Calosoma callidum* Fab.
Staphylinidae
69. *Homeotarsus (Gastrolobium) bicolor* Grav.
70. *Homeotarsus* sp.
71. *Lathrobium (Apteralium) brevipenne* Lec.
72. *L. (Pseudolathra) anale* Lec.
73. *L. longiusculum* Grav.
74. *Rugilus (Stilicus) dentatus* Say
75. *Paederus littorarius* Grav.
76. *Mycetoporus splendidus* Grav.
77. *M. consors* Lec.
78. *Oxyopoda (sagulata)* Erich.?
79. *Philonthus* sp.
80. *Bryoporus rufescens* Lec.
81. *Tachyporus elegans* Horn
82, 83. *Atheta* spp. (2)
84. *Stilicus dentatus* Say
85. *Lobrathium longiusculum* Grav.
86. *Apocellus sphaericollis* Say
87. Subfamily Aleocharinae, unidentified species
Histeridae
88. *Aeletes politus* (Lec.)
89. *Phelister subrotundus* Say
Cantharidae

90. *Cantharis bilineatus* Say
Anthicidae
91. *Notorus* sp.
Elateridae
92. *Aeolus amabilis* Lec.
93. *Melanotus* sp.
Nitidulidae
94. *Glischrochilus fasciatus* (Oliv.)
95. *Phenolia grossa* (Fab.)
Cucujidae
96. *Telephanus velox* Hald.
Cryptophagidae
97. Anomariinae, unidentified species
Phalacridae
98. *Eustilbus apicalis* Welsh
Coccinelidae
99. *Ceratomegilla maculata* DeG.
100. *Hippodamia convergens* Grier
101. *H. 13-punctata* (L.)
Tenebrionidae
102. *Meracantha contracta* (Beauv.)
Scarabeidae
103. *Attaenius* sp.
104. *Onthophagus hecate* Pang.
105. *Phyllophaga tristis* Fab.
Crysomelidae
106. *Coptocycla signifera* (Herbst.)
107. *Lema trilineata* Oliv.
108. *Lina lapponica* (L.)
109. *Diabrotica 12-punctata* Fab.
110. *Disonycha xanthomelaena* (Palm.)
Curculionidae
111. *Hypera punctata* Fab.
112. *Lixus* sp.
113. *Phytonomus nigrirostris* (Fab.)
114. *Sphenophorus* sp.
Diptera
115. Mycetophilidae, unidentified species
116. Phoridae, unidentified species
Hymenoptera
Formicidae
117. *Ponera coarctata pennsylvanica* Buckley
118. *Lasius umbratus mixtus aphidicola* Walsh
119. *L. niger alienus americanus* Emery
120. *Solenopsis molesta* Say
121. *Prenolepis imparis* Say
122. *Camponotus herculeanus pennsylvanicus* DeGeer
123. *Aphenogaster fulva aquia* Buckley
124. *Crematogaster lineolata cerasi* Fitch
125. *Tapinoma sessile* Say
126. *Formica fusca subsericea* Say
127. *F. pallidiflava nitidiventris fuscata* Emery
128. *F. p. schaufussi incerta* Emery
Vespidae
129. *Vespa maculata* (L.)
130. Psammocharidae, unidentified species
Chordata
Amphibia
Ambystomidae
131. *Ambystoma jeffersonianum* (Green)
Bufonidae
132. *Bufo fowleri* Garman
133. *B. americanus* (Holbrook)
Hylidae
134. *Pseudacris triseriata* (Wied)
Reptilia
Colubridae

135. *Thamnophis s. sirtalis* L.
Mammalia
136. *Scalopus aquaticus* (L.)
137. *Microtus pennsylvanicus* (Ord.)

ANIMALS COMMONLY FOUND IN THE CRYPTOZOIC NICHE

Comparison of the taxonomic groups prominent in this and in related studies reveals that most of these animals cannot be considered as true cryptozoa. Since most studies related to this one have been concerned with general soil and litter faunas, many forms not characteristic of the cryptozoic niche are included as are forms occupying this niche only at particular seasons. Certain groups, however, seem to be generally predominant in this niche wherever it has been studied and a brief survey of these forms will indicate the general nature of this type of fauna.

SPECIES NOT STUDIED

The phyla Protozoa, Rotifera, and Tardigrada are apparently widely distributed through soils but will not be considered here because, on account of their microscopic size, they were not investigated in this or in most related studies made by other workers.

SPECIES TYPICAL OF OTHER NICHES

A large number of species often taken in litter are more abundant in some other niche and the majority of these are animals which characteristically inhabit the mineral soil. Nematodes and earthworms fall into this category and are not here classified as cryptozoa although Olson (1928) indicates that some earthworms are more typical of litter than of the soil. A number of arthropods often found under the boards were actually more abundant in the soil and sod than in the cryptozoic niche. This was true of the pseudoscorpions, mites, the unidentified dipluran, psocids, centipedes of the family Geophilidae, a large number of coleoptera, and a variety of lepidopteran, coleopteran, and dipteran larvae. Many of these are well adapted for digging and for subterranean life as, for example, the geophilids which are strikingly tolerant of submergence in water (Chamberlin 1913). Of the coleoptera, the anthicids, elaterid larvae, cucujids, cryptophagids, tenebrionid larvae, and especially scarabeids and curculionids were much more abundant in the soil and humus near the boards than actually under the boards. It was very striking after becoming well acquainted with the fauna to observe how many scarabeids and weevils unknown to the investigator could be found by digging in the nearby sod. Although not here encountered, members of the classes Pauropoda and Symphyla have often been found in the soil and in cryptozoic habitats in various parts of the world (Diem, Thompson, Bornebusch, Williams) but seem to be chiefly associated with the soil itself. Thompson (1924) found the Symphyla increasingly abundant with increased depth.

Animals associated with habitats other than that of

the soil also occur occasionally in the cryptozoic niche. Phalangids and grasshoppers (Acrididae) were sometimes found under the boards but their scarcity in this niche was in striking contrast to their abundance in the surrounding grass. Forms inhabiting the general litter, such as leeches of the family Hirudinidae (Williams 1941) or plant inhabiting forms such as the thysanoptera, certainly cannot be considered a part of the cryptozoic fauna. Similarly, many forms inhabit wood and so are associated directly with logs and debris rather than with the zone of contact between debris and the forest floor. These include many termites, certain ants such as *Camponotus*, and a lepidomatid which occurs under the bark of stumps in the woods where this study was conducted but which was never found under an experimental board.

SPECIES OF SEASONAL OCCURRENCE

A number of animals which do not typically inhabit the cryptozoic niche or feed there may enter this niche in autumn to hibernate and so be of seasonal occurrence. Leaf hoppers (Cicadellidae), and certain spiders, hemiptera, coleoptera, and diptera showed this type of association with the boards. In the studies of Weese and Blake also, hemiptera were characteristic of the litter only in late autumn. Most of the hemiptera hibernating under the boards belonged to the family Lygaeidae and this also seems to be true of many other regions. Dammerman (1937) found the Lygaeidae and Reduviidae to be the most common hemiptera in litter in Malaysia, Grimmet found the Lygaeidae and Aradidae most common in such habitats in New Zealand, and Lindroth indicates that the Tingididae and Lygaeidae are the most common hemiptera in Iceland. Dogel, however, found a predominance of pentatomids in the litter.

A similar constancy seems to hold with respect to other orders of insects. The seasonally occurring coleoptera belonged chiefly to the families Nitidulidae (Ips), Coccinellidae, and Chrysomelidae with one species of cicindelid being a typical spring and autumn resident under the boards. About a dozen dipteran families are commonly mentioned by writers on soil and litter faunas but the three families Cecidomyiidae, Mycetophilidae, and Tipulidae far exceed all others with the families Chironomidae and Simuliidae also receiving frequent mention. Adult dipterans, Mycetophilidae and Phoridae, appeared under the boards in late autumn and larvae were often present. The mycetophilids, however, are more cryptozoic than most seasonal forms because the larvae actually feed in this niche and are more or less typical inhabitants. The adults enter the niche in autumn to oviposit.

CRYPTOZOIC SPECIES ABSENT FROM THE PRESENT STUDY

In the phylum Platyhelminthes, the single turbellarian, subfamily Terricola, is frequently encountered in cryptozoic and litter samples. These "terrestrial

planarians" are particularly important in tropical regions (Dendy 1895, Williams 1941). In the present study only four minute flatworms were recorded and these have not been identified.

One family (Proseriidae) of nemerteans is apparently very prominent in the cryptozoic fauna of Australasia (Dendy 1895) but does not seem to be important in samples taken elsewhere.

Among the arthropods, a number of groups which were not encountered are apparently truly cryptozoic in other regions, primarily in warmer climates. Some termites may be cryptozoic and members of the arachnid orders Scorpionida, Palpigradi, and Pedipalpi live under stones in warm regions. The members of the phylum Onychophora are apparently typical members of the cryptozoic fauna in the local regions where they occur and Dendy includes them in his description of this fauna for New Zealand. Among the crustacea, members of the copepod family Harpacticidae may be found under debris near bodies of water while members of the amphipod family Talitridae seem to be abundant cryptozoic forms in Australasia (Dendy 1895, Grimmet 1926) and in Malaysia where, however, they occur only along the seacoast and at altitudes above 1400 m. (Dammerman 1925). In northern regions amphipods do not seem to be an important part of the cryptozoic fauna except along the seashore.

CHARACTERISTIC CRYPTOZOA

Relatively few taxonomic groups seem to make up the bulk of the cryptozoic fauna in most regions for which information is available. These groups are described below along with certain natural history data on the forms which were important in this study.

Molluscs

Pulmonate gastropods, both snails and slugs, are commonly found in litter and some species are usually typical of the cryptozoic fauna. In this study one species of snail and one slug were characteristic and abundant cryptozoic forms particularly where the soil was moist. Dendy reported snails and slugs as characteristic cryptozoic animals in Australasia, Richards (1928) found them common under dead bark on English heaths, Diem (1903) reported pulmonates in the soil fauna in the Alps up to an altitude of 2250 m., Dammerman (1925, 1937), from collections made in the Malay Archipelago, considers them an essential part of the tropical litter fauna at all levels from the coast to mountain tops and also on small coral islands, Pillai (1922) records them from forest litter in Denmark, and Williams (1941) found them in the rain-forest litter in Panama.

Pulmonates seem to be absent from this fauna in cold regions. Diem failed to find them in the Alps at altitudes above 2250 m. and Anderson & Falk (1935) record no gastropods from the central desert of Iceland. Snails and slugs are associated with moist conditions and with cover such as fallen logs. It was here found, as also recorded by Blake (1926).

and Jacot (1940), that the number of molluscs decreased with dry conditions largely as a result of vertical migration into the soil. Pillai (1922) recorded an increase in molluscs in the wet fall weather. Dogel (1924) found that slugs and snails were not present in sandy soils in the neighborhood of Leningrad, U.S.S.R., and Adams (1915) states that logs largely determine the presence of land molluscs. In Bornebusch's study and in the present study, certain differences in the local distribution of gastropods were correlated with soil type and amount of moisture and surface debris.

Although all of the molluscs found in litter belong to the suborder Stylommatophora, most of the smaller taxonomic groups are not of particularly wide distribution. Dendy, in fact, commented on the tendency of molluscs to form highly endemic faunas. *Deroceras agreste* (= *Agriolimax agreste*), the slug found in this study, is a common European form and has received attention as an agricultural pest (Miles, Wood, & Thomas 1931, Carriek 1942). It is highly omnivorous, feeding chiefly on the leaves of plants but also attacking roots and stems and apparently feeding to some extent on general humus. It spends the daytime in the cryptozoic niche but may come out onto plants to feed at night or, in very wet weather, even in the daylight.

The eggs are sometimes deposited in wet soil but are generally deposited in small clumps in the cryptozoic niche where they require several months to mature.

No predators were seen to eat *Deroceras* although they are said to be eaten by birds, moles, toads, and shrews (Miles *et al.* 1931) and also by carabids and staphylinids (Theobald 1905).

Slugs are very sensitive to dry conditions and hot dry weather reduces viability, mating, and oviposition. They are resistant to cold weather and will remain active and continue to breed in near-freezing temperatures. Miles mentions them as migrating vertically in winter as well as in very dry weather and this has also been observed by the writer. They will, however, survive solid-freezing near the soil surface.

Retinella rhoadsi was much the most abundant species of snail encountered and is the only one considered in the quantitative counts. It is probably a fungus feeder and seems to be found only in rotten logs or in the cryptozoic niche. In winter small aggregations of these snails could be found by digging in the soil under the boards.

Isopods

Isopods of the suborder Oniscoidea are very important members of the cryptozoic fauna in many widely separated parts of the earth. In the present study the species *Trachelipus rathkei* (= *Porcellio rathkei* = *Tracheoniscus rathkei*) was perhaps the single most characteristic cryptozoic species, while the form mentioned by Dendy as typical for Australasia is the closely related *Porcellio graniger* and a species of *Porcellio* was common in the Brodskys'

samples from Turkestan. Similarly, the genus *Trichoniscus* occurs in New Zealand (Grimmet), Denmark (Bornebusch), Panama (Williams), and also in Eastern North America, while *Oniscus*, which occurs in the United States and continental Europe, is also mentioned by both Dendy and Bornebusch, and the closely related *Alloniscus* was a constant and typical element in Dammerman's Malaysian studies although he found isopods to be less abundant at altitudes above 3000 m. In all of the woodlands of the Chicago region some species of isopod seems to be one of the most conspicuous cryptozoic animals. It is interesting to note that one of the factors which led Grimmet to suspect a wide difference between the woodland faunas of New Zealand and the United States was the fact that Shelford (1913a) makes little mention of terrestrial isopods.

Trachelipus is a very general feeder and will survive almost indefinitely on decaying wood or, in the laboratory, even on wet paper towels.

Eufonia, *Galerita*, and *Anomoglossus* have been seen to eat young isopods, and ants (*Formica*) have often been seen carrying dead isopods although these may have died before being found by the ants. Brooks (1942) states that some ponerine ants prey on isopods. Repeated observations have failed to support the common assumption that these isopods are preyed upon by centipedes. In hours of watching the animals under a dim red light in the laboratory, *Lithobius* has been seen to devour innumerable collembola and perhaps other minute forms such as psocids and mites but was never seen to attack either adult or immature *Trachelipus* even when these were abundant and were frequently encountered by the centipedes.

These isopods form large aggregations under the influence of environmental conditions and a number of studies of animal behavior have been concerned with this problem (Allee 1926, Gunn 1937, Waloff 1941). The methods by which aggregations are formed on a dry substratum have been well described by Allee (1926) and such an aggregating tendency may have survival value in reducing evaporation from the body.

Isopods are generally negative to light and seldom wander outside the cryptozoic habitat in the daytime. However, Abbot (1918) found this reaction in *Porcellio* to be somewhat variable and records a case when the ground was flooded and the isopods were to be found in the daytime on green plants several feet above the ground. The writer observed this same thing on September 16, 1942. The ground was very wet, the temperature was 27.5 C., the relative humidity was 80 percent, and the day was bright but cloudy. Several isopods were seen on oak trees at heights up to 1.5 m. and one individual which was watched remained practically motionless for over one hour. It then descended the tree trunk and disappeared into the grass.

When tested in the humidity gradient, *Trachelipus* showed no tendency to approach either the wet or

the dry end but moved about at random with individuals at the dry end of the apparatus dying more rapidly than the others.

Active isopods were several times found under boards where the temperature was 0° C. and in the laboratory they will remain active overnight at a temperature of -1° C. However, a very slight decrease from this temperature is rapidly lethal. In one test of twenty individuals, ten were killed by an exposure of one hour to -2.6° C., and in twelve attempts only one individual survived an exposure of one hour to a temperature of -4.5° C.

No striking heat conservation by aggregations of *Trachelipus* was demonstrable in the laboratory. In a sealed half-pint vacuum bottle exposed to a temperature of 4° C., the temperature of 27 adult isopods fell to 9.2° C. in 17.5 hours while the air temperature in another bottle, known to provide equivalent insulation, fell to only 8.5° C. The difference in specific heat between the isopods and air probably accounts adequately for the difference in final temperature.

Apparently the cold weather of early winter is a critical time for *Trachelipus* which is active down to -1° C. but must migrate vertically into the soil before the temperature falls another two or three degrees. On December 10, 1942 following a very cold night which froze all of the boards solidly to the ground, the isopods were found aggregated in holes under the boards, most of them at a depth of about 5 cm. at which depth the soil temperature was 4° C.

Newly hatched isopods appeared in early spring (May 25 in 1942) and they seemed to emerge in several waves, reaching a maximum about August 2 and continuing until frost. The last group recorded in 1942 was on August 27. Grimmet (1926) noted an autumn and winter increase in isopods coinciding with periods of increased rain.

Isopods migrate vertically when the soil becomes dry, as noted by Bornebush, but in this study they were almost never found burrowed in the soil except under a board. Thus they escape unfavorable conditions by migrating from the cryptozoic niche to the subterranean niche. Miller (1938) found the optimum relative humidity for terrestrial isopods to be 100 percent.

At night isopods may be found moving about in the grass but there is no nocturnal mass exodus from the cryptozoic niche such as shown by the slugs. Most of the isopods found under boards in the daytime will still be found there at any hour during the night.

Spiders

Spiders were of very common occurrence under the boards, particularly in the autumn when many species descended from the above vegetation. Most species were represented by one or few individuals and have not been identified. The families Lycosidae, Argiopidae, Thomisidae, and Clubionidae were apparently best represented but this observation is somewhat qualitative. The families Lycosidae and

Clubionidae were prominent in Grimmet's collections in New Zealand and Dogel took many lycosids in the soil in Russia as did Dammerman in Malaysia. Spiders may descend to considerable depths in the soil and argiopids and lycosids were found by Motter (1898) in coffins exhumed after several years burial in Washington, D. C.

For the purposes of this study the spiders have been lumped into a single group because the data are inadequate for considering families or species individually and because all of the spiders are predacious.

Spiders always attained maximum numbers in the autumn and many juvenile forms were found. The number of spiders under the boards also increased in dry weather. Lowrie (1942) states that the substratum and humidity are the most important factors controlling the distribution of spiders and Weese (1924) found that most spiders are unable to complete their development or to emerge except under conditions of high humidity. Many adolescent spiders also hibernate in the ground and in decaying logs. Probably some spiders do typically prey on cryptozoa but the data of this study are inadequate to designate any truly cryptozoic spiders.

Chilopods

Chilopods are very characteristic in soil, litter, and cryptozoic habitats nearly everywhere although not recorded by Anderson & Falk from Iceland. In the present study and that of Pearce (1943) they were found more in litter than in the soil, and Adams (1915) considers them as characteristic members of the "humus and rotten log communities." However, chilopods do occur in the soil outside of the cryptozoic niche, and they migrate vertically, especially in dry weather. Geophilids were not uncommon in the soil of these woods but only one individual was taken from under a board so this family is here considered as belonging to the hypogeous fauna.

Lithobiids were found most commonly under boards although also occurring in the soil, and they probably represent forms ranging between the hypogeous and cryptozoic faunas. Dendy listed chilopods as characteristic cryptozoic animals in Australasia, Bornebush found them in soil and litter in Denmark, and Thompson found lithobiids and geophilids in arable land in England. The same two families were characteristic of Diem's alpine studies and Grimmet's work in New Zealand, and chilopods were invariably an element in Dammerman's Malaysian studies where they occurred in all habitats from the rain forest to barren coral islands. It appears that the families Geophilidae and Lithobiidae are characteristic of soil and surface faunas over much of the world and that the lithobiids are more associated with the cryptozoic habitat. Many of the genera and species are widespread. *Lithobius forficatus*, the common centipede in this study, was found by Thompson in England and its range also includes continental Europe and South America.

As already stated, the indications are that this

species feeds primarily on collembola and other minute forms. There were no indications that they eat either roaches or isopods although they are cannibalistic and the writer has twice found *Lithobius* under boards swallowing smaller members of its own species. Thus they are capable of taking fairly large food. Like the roaches, the majority of the centipedes leave the cryptozoic niche in late autumn and hibernate in decaying logs or beneath bark where they may form hibernating aggregations. One such aggregation found by the writer in a decaying log contained nineteen adult *Lithobius*. Thus an animal which is usually described as solitary may show some social traits in autumn and winter. An aggregation of nine adult *Lithobius* was found under a board in October, 1942.

Immature *Lithobius* usually were found under the boards from about mid-August until mid-September. In 1942 they occurred from August 27 until September 12.

In the humidity gradient *Lithobius* always moved rather rapidly to the most humid compartment and remained there motionless. On the paper substrate they appeared not to differentiate between wet and dry halves. Despite their positive reaction to moist air, centipedes occurred about equally in the grazed and ungrazed portions of the woods.

Diplopods

Diplopods, like chilopods, are characteristic of litter and cryptozoic faunas over much of the world. As mentioned by Jacot, they are more typically found under debris and stones than in soil and so are more cryptozoic than the chilopods. Although many families of diplopods occur in such habitats, the two families Julidae and Polydesmidae seem to be most typical and are usually encountered in studies of the fauna of litter and debris. The julids seem to require more specific habitat conditions than the polydesmids and so are less generally distributed. Jacot found julids particularly common in moist woodlands especially where the soil was not too compact, and Bornebusch found them associated specifically with mull soils. Dammerman (1925) found the Julidae characteristic of small islands near Java and the family is also mentioned for New Zealand by Grimmet and by Pillai for Bavaria. Julids are common cryptozoic animals in many woodlands near Chicago and, in fact, in the wet area mentioned earlier on the farm where this study was conducted, but they were rare in the area studied. The polydesmids, on the other hand, were found by Bornebusch to be independent of soil type and they seem to be much more generally distributed. They were abundant in this study and have been reported in nearly all studies which reported julids. Diem, Dogel, and Pfitzen recorded polydesmids but not julids.

One species, *Scytonotus granulatus*, made up well over 90 percent of the diplopods encountered and only this species was used for quantitative analysis.

Scytonotus was one of the most characteristic of the cryptozoa but also occurred, although less abun-

dantly, in the soil. It is apparently a very general feeder utilizing nearly any kind of organic matter such as plant roots, decaying wood, and acorn husks. They are also scavengers and have several times been found feeding on dead isopods. In the laboratory the writer has twice seen these diplopods attacked and killed by carabid beetles (*Galerita*) but in both cases the diplopod was dropped immediately and not eaten. The indirect evidence relating to predation on this species by spiders will be discussed later.

In the humidity gradient *Scytonotus* tended to move to the moist end as does *Fontaria* (Shelford, 1913). On humid nights in the field the *Scytonotus* would frequently emerge and form aggregations on the upper surfaces of the boards. The largest such aggregation recorded was found at 2:00 A.M. on August 21, 1942 when 57 *Scytonotus* were on top of one board. All had moved back under the board by 6:00 A.M. although such aggregations sometimes remained in shaded spots until after 7:00 A.M. These diplopods were seldom found out wandering in the grass and, although they were sometimes seen on fence posts and tree trunks, they were not seen to eat green vegetation or to leave the cryptozoic niche to feed.

The eggs evidently hatched in late June and by late July it was unusual to find a fully grown adult. In 1942 newly hatched *Scytonotus* were first found on June 12 and by July 31 very few adults were found. The juvenile forms mature rapidly and in the autumn most of the *Scytonotus* encountered were adult. However, newly hatched individuals were still present in one area on September 3, 1942. It is possible that the adults mature in autumn and hibernate in the soil under the boards, dying after breeding in the first half of summer.

Collembola

Collembola are usually abundant in soil surface and litter samples but were not recorded in the Brodskys' samples from an arid region. Thompson (1924) found that collembola and acarina make up most of the fauna of arable land while others, especially Bornebusch, have noted a reciprocal relationship in the abundance of mites and collembola varying with soil and humus type. In this study collembola were much more abundant than mites and were characteristic particularly of the cryptozoic niche although often migrating vertically into the soil. Many genera are very widely distributed. The one genus of sminthurid encountered (*Ptenothrix*) is also reported by Handschin (1925) from Java and Sumatra. The entomobryid genera *Entomobrya* and *Tomocerus* which were the most common collembola in this study are also recorded from Java and Sumatra by Handschin, by Bornebusch from Denmark, by Diem from the Alps, and by Lindroth from under stones in Iceland. *Isotoma viridis* is cosmopolitan although Diem found it replaced by another species of *Isotoma* (*I. palustris*) at the highest altitudes in the Alps.

The five species of collembola have been lumped

into a single group for analytical purposes because of the difficulties of identification under field conditions and because no really satisfactory census method was devised.

The collembola are primarily feeders on decaying organic matter, soil humus, fungus, and fungus spores (Mills, personal communication) although some species are predacious (Macnamara 1924). Mites, staphylinids, nematodes, dipterous larvae, *Lithobius*, and spiders are among the forms which have been mentioned as predators of collembola (Mills, Macnamara 1919, Ford 1937) and the writer's observations suggest that *Lithobius forficatus* subsists largely on collembola.

Most collembola are non-tracheate, respiration being cutaneous, and are extremely sensitive to low humidity (Macnamara 1924). Davies (1928) found for every species tested in a humidity gradient that the optimum relative humidity was 100 percent although specific differences existed in ability to survive in dryer air. The resistance of collembola to drying is also increased if there is a film of moisture on the surface with which they are in contact.

Many collembola apparently survive high temperatures only in the egg stage (Folsom 1923) so maximum adult populations tend to be attained in winter (Bornebusch, Ford 1937). Oviposition is said to occur only in darkness (Macnamara 1919) and may be restricted to a particular season of the year.

Collembola escape unfavorable conditions in the cryptozoic habitat by migrating vertically along holes left by roots or by burrowing animals and these migrations may occur daily as the soil dries locally (Davies 1928, Volz 1934). Some vertical migration also occurs in response to frost, although collembola generally survive being frozen solid. Some species are active all winter even in cold regions and the life span of an individual may exceed one year (Macnamara 1924).

Collembola populations may respond very rapidly to favorable conditions as the eggs of some forms hatch in from six to ten days after oviposition (Lubbock 1871). Populations were found to increase conspicuously with increased soil moisture as also noted by Ford (1937). *Ptenothrix* was very rare in the grazed portion of the woods and was never found under boards before mid-July. *Tomocerus* first appeared in 1942 on August 2 and thereafter became more abundant on each trip up until the time of frost.

Orthoptera

The most common orthopterans in the cryptozoic habitat were the Blattidae, although the distribution of roaches was largely controlled by specific local conditions such as grass height. Roaches tend to select larger pieces of debris for shelter so they are not especially common in ordinary soil and litter collections. Crickets were also cryptozoic, especially in the autumn and in the same areas as the roaches. Dammerman (1937) lists one gryllid as character-

istic of the detritus fauna. Other orthoptera were never common under the boards.

Parcoblatta is very omnivorous, being primarily a scavenger on both animal and vegetable debris and also a very minor predator (Blatchley 1920).

Roaches are eaten by toads (*Bufo*) and the writer has seen young nymphs eaten by large carabids (*Galerita* and *Euferonia*). Blatchley states that both larval and adult carabids eat many orthoptera.

Mating takes place in early summer, the newly hatched young appear in August, and the winter is passed in the nymphal stage. When cold weather appears, many roaches leave the cryptozoic niche and move into rotten logs or under the bark of stumps where the winter is passed in large aggregations. A few descend into the soil and may come to the surface on warm winter days. Two very sluggish roaches were found under one of the boards on January 15, 1944 after a period of unusually warm weather. Roaches survive very cold weather. In one experiment four *Parcoblatta* were kept at a temperature of -21° C. for 24 hours and the two which survived recovered normal motility within 20 minutes after removal from the freezing chamber.

When roaches were brought into the laboratory and placed on a partially wet substratum they showed no discrimination between wet and dry areas but scattered at random over the available space. When tested in the humidity gradient they definitely avoided atmospheric humidities above about 60 percent R.H. and were extremely tolerant of dry air. Some individuals were still alive after 75 hours exposure to a relative humidity of approximately 11 percent. Figure 1 shows the autoselected humidities for 69 roaches tested in the humidity gradient apparatus. The association of roaches with the grazed portion of the woods is possibly attributable to the lower humidity under boards lying on soil with a low water-holding capacity.

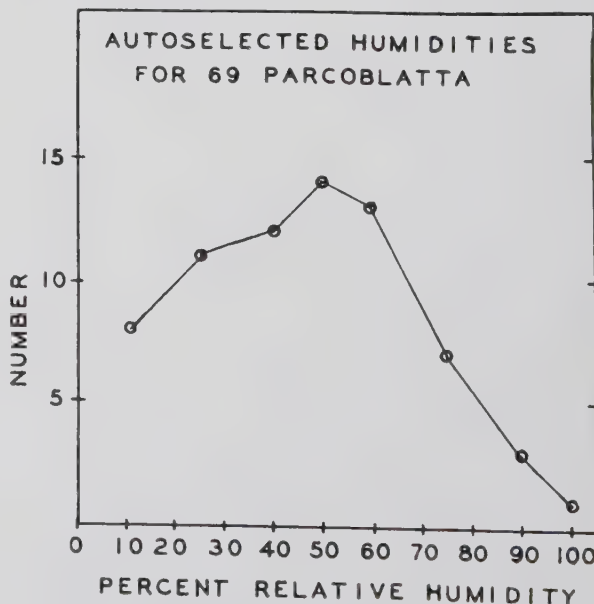


FIG. 1. Autoselected humidities for 69 *Parcoblatta*.

Crickets are also very omnivorous. They are cannibalistic and eat dead insects as well as grass and other vegetation. They probably have many predators and the writer has on many occasions found carabids (*Euferonia* and *Searites*) eating young crickets.

In the Chicago region crickets pass the winter as eggs and the adults appear in late summer. They always appeared earlier in the grazed portion of the woods than in the ungrazed part. In 1942 the first crickets appeared in the grazed portion on June 12 and none was found under boards in the ungrazed portion until July 30. Crickets were always most abundant in association with short grass and with the grazed portion of the woods but they were less confined to these situations than were the roaches.

Gryllus spent much of the daytime under boards, particularly on sunny days, but at night they often left this niche to feed. In autumn the large females moved under the boards to oviposit and died there, presumably killed by the cold weather. Scavenging ants were frequently found feeding on these dead females.

Dermaptera

No dermapterans were taken although earwigs appear to be true cryptozoa in other woodlands in the Chicago region. Many of the forficulids are cosmopolitan and probably are often typical members of the cryptozoic fauna. Their absence from these woods is of some interest.

Coleoptera

Coleoptera are almost always found in soil, litter, and cryptozoic habitats although Dammerman (1937) found beetles absent from certain coral islands near Java. With so many families and genera of coleoptera it is rather startling to find the same groups mentioned repeatedly by authors writing on soil and litter faunas in various parts of the world. In the present study the families Staphylinidae, Carabidae, and Histeridae were typically common under the boards while other forms not typical of the cryptozoic niche were only common in autumn and spring.

In Table 3 are listed coleopteran families which have been mentioned as particularly abundant or characteristic from a number of studies. It will be noted that the carabids and staphylinids are usually a predominant part of the fauna although Dammerman found that, in the tropics, these two families are of reduced importance in the lowlands. In many cases the same genera are prominent in widely separated regions. The genus *Notiophilus* (Carabidae) was prominent in the studies by Cole, Lindroth, Pillai, Brodsky, Bornebusch, Pearse, and Buckle, and many of the staphylinid genera are of similarly wide distribution. Four of the twelve most common genera of carabids found by Bornebusch were also found in the present study and, of the twelve most common genera of staphylinids taken by Bornebusch, five were also common under boards at Plano. Both carabids and staphylinids were nearly as common in the litter and sod as under the

TABLE 3. The important coleopteran families in various studies.

Study	CRYPTOZOIC				NON-CRYPTOZOIC OR SEASONAL					OTHERS
	Carabidae	Staphylinidae	Histeridae	Pselaphidae	Elaterridae	Scarabaeidae	Curculionidae	Tenebrionidae	Coccinellidae	
Cole										Chrysomelidae
Illinois.....	X	X	X		X	X	X	X	X	Cucujidae
Lindroth										Nitidulidae
Iceland.....	X	X		X	X	X	X			Cucujidae
Dogel										
Leningrad.....	X	X	X		X	X	X	X	X	
Dammerman										
Malaysia.....	X	X		X	X	X	rare	X		Seydmaenidae
Pillai										Cleridae
Bavaria.....	X	X			X	X	X	X	X	Ipidae
Pfetten										
Bavaria.....	X	X		X	X		X	X	X	Cantharidae
Bornebusch										Nitidulidae
Denmark.....	X	X			X		X		X	Ptiliidae
Brodsky										Cantharidae
Turkestan.....	X	X	X			X	X	X	X	Anthicidae
Pearse										
N. Carolina....	X	X		X	X	X	rare	X	rare	Chrysomelidae
Thompson										
England.....	X	X		X		X				
Grimmet										
New Zealand...	X	X		X	X		X			Ptiliidae
Williams										Ipidae
Panama.....	X	X	X	X	X	X	X	X		
Buckle										
England.....	X	X			X					

boards, so these two families, while typical of the cryptozoic habitat, must be considered as overlapping the general soil and litter fauna.

Two species of histerids were found to be characteristically cryptozoic but the family is not commonly recorded as an important part of the litter fauna. Pselaphids are apparently important cryptozoic forms in many regions and it seems somewhat surprising that none was taken. Table 3 seems to suggest a reciprocal relationship between the families Histeridae and Pselaphidae.

The other coleopteran families listed in Table 3 are not really characteristic of the cryptozoic niche. The table indicates, however, a striking constancy of the coleopteran fauna not only of the cryptozoic habitat but also of the soil and litter habitats in various parts of the world.

For quantitative analysis the species *Aeletes politus* was the only histerid considered because it represented about 90 percent of the histerids encountered. This species is actually smaller than some of the collembola and its function in the dynamics of the fauna is probably that of a scavenger rather than a predator.

The staphylinids were considered as a single group largely because of the difficulty of distinguishing species in the field. These beetles are important predators and scavengers in the cryptozoic niche although they were fully as abundant in the humus layer of the soil as under the boards. Thus, like the large carabids and centipedes, they represent forms which overlap two habitats. The two most abundant and characteristic forms were *Apocellus sphaericollis* and *Philonthus* sp., both of which generally occurred in small colonies and sometimes

formed large aggregations. Philonthus was only abundant in this niche in autumn. Staphylinids were frequently found feeding on dead crickets and carabids and it seems likely that they are more important in the cryptozoic fauna as scavengers than as predators.

For quantitative purposes the carabids have been divided into two categories on the basis of size. The category "large carabids" consists of the following forms: *Euferonia*, *Galerita*, *Calasoma*, *Scarites*, *Harpalus vagans*, *Anomoglossus*, *Dicaelus*, and *Anaferonia*. Of these, *Euferonia stygica* was generally the most abundant, with *Scarites substriatus* being second in 1942 but being almost entirely replaced by *Harpalus vagans* in 1943. The "small carabids" consisted of *Harpalus vulpeculus*, *Platynus*, *Calathus*, *Pristodaetyla*, and *Notiophilus*, with *Harpalus* and *Calathus* being far more abundant than any of the others.

These carabids are predacious although they may eat plant material to some extent (Buckle 1923). The larger forms are probably more effective as predators, are less confined to the cryptozoic niche than are the small carabids, and show a different type of seasonal and spatial distribution. Therefore, the assumption is made that each of these categories is relatively homogeneous and distinctive. The difficulties of field identification and the small numbers of individuals precluded separate analysis of each carabid species.

In summer, when the grass provided shelter, the large carabids were nearly as abundant in the sod as under the boards. Thus they apparently overlap between the hypogeous and the cryptozoic faunas. Nevertheless, they are probably the most important cryptozoic predators in this region and might be expected to exert a considerable influence on this fauna. These beetles dig short burrows, usually from one to five cm. deep, and were often found quiescent in these holes under boards.

The greatest increase in the cryptozoic population of large carabids approximately coincided with the appearance of newly hatched roaches and the beetles feed on these to some extent. However, they are euryphagous and their distribution with respect to experimental areas indicates that their populations were not closely integrated with the roach population.

These carabids showed no apparent discrimination between wet and dry substrata although in the humidity gradient they moved fairly rapidly to the moist end and remained there, motionless. Hamilton (1917) also found that carabids move to the moist end of a humidity gradient.

Breeding apparently continues throughout the summer. In 1942 copulating *Euferonia* were recorded on April 22, May 6, June 25, July 4, July 8, July 25, August 3, August 27, and September 16.

These beetles are also cannibalistic and the writer has several times seen one of them feeding on the remains of another. In the cold weather of spring and autumn, however, they tended to be found together in small aggregations often containing more

than one species. They hibernated both in the ground and in decaying logs. From an aggregation in one decaying log in winter the writer took twelve large carabids.

The small carabids were much less abundant than the larger forms and the data on them are less complete. They tended to form small aggregations in winter and many left the cryptozoic niche to hibernate in decaying logs. Copulation was most frequently observed in the autumn and eight copulating pairs were found on September 18, 1942. Small carabids were often found out in the grass at night but seldom seemed to leave the shelter of the boards in the daytime.

Ants

Ants are often a very characteristic part of the cryptozoic fauna. In many studies of litter faunas, as well as in this study, the ants were much the most abundant of the larger organisms. Many genera are very widely distributed. Of the nine genera found in the present study, eight occurred in Pearse's study in North Carolina, five were found by Dammerman in the Malay Archipelago, and three by the Brodskys in Turkestan, while only the genus *Camponotus* occurred in common with Williams' study in Panama. Like the termites, the local *Camponotus* is typically a wood-inhabiting form and many of the other ants seemed to be as common in the general litter and grass as in the cryptozoic habitat. Ant colonies alter the habitat under a board and they must be an influential factor in the cryptozoic fauna of many places. Ants are not reported either by Anderson & Falk or by Lindroth from Iceland and Dammerman found that they do not occur at elevations above 2000 m. in Malaysia. Thus their presence in the cryptozoic fauna is more variable than that of the coleoptera.

The most common ants were *Lasius niger*, a species that occurred in this woods as often under leaves as under boards, the three species of *Formica*, and *Crematogaster lineolata* which seemed to be the most typically cryptozoic species. The role of the ants is probably chiefly that of scavengers (Wheeler 1913).

The habitat relationships of all species encountered in this study have been described by Talbot (1934). She finds that *Formica pallidifulva schaufussii incerta* is more tolerant of xeric conditions than is the subspecies *nitidiventris fuscata* and the present study corroborates this observation in that *schaufussii* was more common in the grazed portion of the woods where the soil had a lower water-holding capacity.

Formicas were often seen carrying dead animals of other species and when large *Formica* colonies occurred under boards they tended to drive out most other animals. Collembola were characteristically absent from these boards and it is possible that some of the ants act as predators.

There also seemed to be a tendency for the ants to be more common under the boards which received most sunlight but the data are inadequate for analysis of this factor.

Vertebrates

Vertebrates such as mice, moles, snakes, lizards, and amphibia may enter the cryptozoic niche but are usually not true members of this fauna. It seems probable, however, as suggested by Dendy, that certain amphibia should be considered as true cryptozoa. Frogs and toads were seasonal residents under the boards in wet weather but elsewhere in the Chicago region salamanders, particularly *Plethodon cinereus*, typically inhabit the cryptozoic niche and lay their eggs there.

RELATED FAUNAS

A number of animal habitats, including the cryptozoic habitat, have as their primary characteristic the provision of shelter from light, high temperature, air of high drying power, and, to a less important extent, from such factors as wind and precipitation. Such shelter is to be found in the mineral soil, in caves, and in the interior of logs and stumps. In wood, however, this shelter is only available, at least in the early stages of decay, to animals capable of penetrating this material. Savely (1939) has studied the ecological succession of animals in dead logs from soon after cutting until the logs were well decayed and merging into the forest floor. His study reveals a fauna which has many species in common with the cryptozoic fauna but with a different group of characteristic forms which are largely wood-eaters. In general, as succession proceeds, the fauna more nearly approaches the cryptozoic fauna which is characterized by forms which inhabit the niche chiefly for the shelter which it provides. In caves, as in the cryptozoic niche, the characteristic forms are chiefly scavengers and predators but the true cavernicolous faunas are quite distinct from the cryptozoic fauna. Racovitza (1907) has drawn a distinction between the cave fauna and the hypogeous fauna on the basis of degree of morphological modification.

The shelter obtainable by burrowing into mineral soil is largely restricted to forms capable of digging and of tolerating occasional flooding of the habitat and an atmosphere low in O_2 and high in CO_2 although the typical cryptozoa may penetrate to considerable depths along holes left by earthworms, burrowing mammals, or decayed roots. As found by Thompson (1924) for collembola, many cryptozoa will descend more deeply into loose and well aerated soil. The fauna of this study bears some remarkable resemblances to that studied by Motter (1898) in an unusual investigation of the fauna of 150 human bodies disinterred after several years burial at a depth averaging over 1.5 m. in a Washington, D. C. cemetery. He found earthworms, four species of gastropods, isopods, nine genera of mites, and five genera of myriopods including *Lithobius* and *Julus*. The numerous insects included collembola, termites, nine families of coleoptera (including carabids, pselaphids, staphylinids, nitidulids, elaterids, scarabids, and curculionids), eight families of diptera

(including Mycetophilidae and Phoridae), and eight genera of ants. In all he obtained no fewer than fourteen genera which were also encountered in the present study. The most abundant beetles were staphylinids. While it is clear, as pointed out by Dendy, that no sharp dividing line can separate the cryptozoic fauna from the fauna of the soil, the two are normally quite distinct during the summer months and where the soil has not been subjected to mixing which increases aeration and distributes organic matter to unusual depths.

There is also a seasonal interchange of species between the cryptozoic niche and other niches. Forms which typically live in vegetation or along the forest margin during the summer may appear in the cryptozoic habitat in the autumn and many typical cryptozoa descend into the soil in winter or move to hibernacula under the bark of stumps. Thus, although the cryptozoa form a distinctive fauna characterized by a peculiar combination of typical forms, there is an overlapping of some animals between the cryptozoic and other habitats and also a seasonal interchange of animals with other niches.

With respect to food supply, the fauna of any niche may be roughly divided into key-industry forms, those which convert available organic matter into animal protoplasm, and associated forms which are largely predators, parasites, and scavengers. In decaying logs many of the key-industry forms are wood-eaters while the true hypogeous fauna contains numerous forms such as many scarabid and elaterid larvae which feed upon the roots of vegetation. Such food sources are largely absent in the cryptozoic niche and the key-industry forms tend to feed on the general humus or to be very omnivorous. In addition, some fungus feeders such as mycetophilid larvae and many snails are able to feed on molds growing in this niche while others such as ants may live in the cryptozoic niche but obtain their food supply by foraging outside.

GENERAL FAUNAL FEATURES

The total number of inspections of boards recorded in this study was 8,380 and the total number of animals was 129,654. It must be remembered that the count of ants was subject to considerable error and that certain forms such as collembola, acarina, nematodes, psocids, and cicadellids were not counted at all. Other atypical or rare forms such as earthworms and diplurans have been omitted from the following table (Table 4) which shows the relative abundance of the important groups of animals. The only really important and typical forms omitted are the collembola.

Table 4 indicates the extent of observations but not the true composition of the fauna at any one time or place. Some of the forms included are present only at a particular season or in a particular part of the locality studied and some are not truly cryptozoic. In Table 5 the more typically cryptozoic forms are grouped according to food habit.

TABLE 4. The total numbers of animals counted.

Form	Total Number	Percent of Total	Percent of Total (Omitting ants)
Trachelipus.....	18,741	14.45	49.71
Diplopods.....	2,462	1.90	6.53
Deroceras.....	1,598	1.23	4.24
Large carabids....	919	0.71	2.44
Small carabids....	395	0.30	1.05
Lithobius.....	676	0.52	1.79
Spiders.....	964	0.74	2.56
Staphylinids.....	821	0.63	2.18
Histerids.....	424	0.33	1.13
Parcoblatta.....	3,317	2.56	8.80
Gryllus.....	4,623	3.57	12.26
Retinella.....	1,199	0.92	3.18
Nitidulids.....	138	0.11	0.37
Myodochus.....	244	0.19	0.65
Telephanus.....	50	0.04	0.13
Coccinelids.....	149	0.11	0.40
Curculionids.....	33	0.03	0.09
Adult diptera.....	92	0.07	0.24
Wasps.....	10	0.01	0.03
Meracantha larvae	23	0.02	0.06
Other larvae.....	795	0.61	2.11
Amphibia.....	16	0.01	0.04
Other vertebrates.	7	0.01	0.02
Ants.....	91,957	70.92	

TABLE 5. Numbers of cryptozoa grouped according to food habits.

Form	Total Number	Percentage
Trachelipus.....	18,741	
Gryllus.....	4,623	
Parcoblatta.....	3,317	
Diplopods.....	2,462	
Histerids.....	425	
Total omnivores and scavengers.	29,568	81.82
Spiders.....	964	
Large carabids.....	919	
Staphylinids.....	821	
Lithobius.....	676	
Small carabids.....	395	
Total predators.....	3,775	10.44
Deroceras.....	1,598	
Retinella.....	1,199	
Total plant and fungus-eaters...	2,797	7.74
Total.....	36,140	100.00

It is evident that much the greatest part of the cryptozoic fauna consisted of scavengers or very general feeders. If the data were complete this class would be even larger as the collembola belong here. Also, although the staphylinids are listed as predators, it is certain that they are also scavengers to a considerable extent.

Inclusion of the ants in Table 5 brings the omnivores and scavengers up to 94.87 percent of the entire fauna showing that the cryptozoic niche is inhabited primarily by animals which can utilize the general organic matter found there. The faunas of humus and soil contain many forms which feed primarily on plant roots, fallen seeds, and similar plant material and the fauna of logs includes wood-eating

forms. It seems to be this primarily euryphagous nature which delimits the cryptozoic fauna from the other faunas related to it by the requirements of their typical members for avoiding exposure to the full impact of outside environmental conditions.

Forms entering the cryptozoic niche seasonally for hibernation or oviposition do not to any great extent feed within the niche and they make up a very heterogeneous group with respect to food habits. The faunal picture would be greatly confused if, for example, we were to include the phytophagous cicadellids and the predacious coccinelids as cryptozoa on a par with the isopods and roaches.

Certain forms were demonstrably more abundant in the sod near the boards than actually under the boards. Table 6, which represents the results obtained on a single day, will serve as an example of such data. An attempt was made to count all of the animals in Areas X and N (30 boards) and, in addition, at a distance of about 30 cm. from each board an area of sod the size of the board was searched for animals to a depth of about 3 cm.

Table 6 is quite typical of the picture obtained on a day when the ants are out foraging. The more typically cryptozoic forms have been placed at the head of the list and it will be seen that they are for the most part readily distinguishable by means of

TABLE 6. Relative abundance of various animals under boards and near boards on October 21, 1943.

Form	Under boards		In nearby sod	
	Number	% of total	Number	% of total
Trachelipus.....	21	3.37	7	1.69
Collembola.....	255	40.93	42	10.17
Deroceras.....	11	1.77	2	0.48
Scytonotus.....	27	4.33	19	4.60
Large carabids.....	14	2.25	4	0.97
Small carabids.....	4	0.64	0	
Spiders.....	15	2.41	4	0.97
Retinella.....	13	2.09	0	
Parcoblatta.....	20	3.21	0	
Lithobius.....	8	1.28	0	
Frog (Pseudacris)...	2	0.32	0	
Histerids.....	23	3.69	0	
Gryllus.....	4	0.64	2	0.48
Myodochus.....	9	1.44	0	
Lasius niger.....	51	8.19	20	4.84
Aphenogaster.....	11	1.77	30	7.26
Crematogaster.....	7	1.12	4	0.97
Cremata subsericia....	62	9.95	2	0.48
Cucujids.....	13	2.09	33	7.99
Staphylinids.....	6	0.96	11	2.66
Mites.....	26	4.17	143	34.62
Curculionids.....	0		2	0.48
Scarabeids.....	0		3	0.73
Adult diptera.....	5	0.80	8	1.94
Diplurans.....	1	0.16	3	0.73
Coccinelids.....	1	0.16	1	0.24
Larvae.....	4	0.64	4	0.97
Earthworms.....	6	0.96	48	11.62
Nematodes.....	4	0.64	15	3.63
Pseudoscorpions.....	0		6	1.45
Total.....	623		413	

TABLE 7. Numbers of animals per 100 boards by areas.

Area..... No. Stations..... Inspections.....	UNGRAZED					GRAZED								MEAN % OF TOTAL	
	H 20 1550	X 15 630	TP 121 1247	Misc. 37 489	Mean 193 3916	A 20 901	B 40 1368	C 20 503	D 20 648	O 44 856	Misc. 32 188	Mean 176 4464	Un- grazed	Grazed	
Trachelipus.....	372.84	484.60	384.44	269.33	381.59	109.54	140.57	44.73	65.74	4.26	106.91	85.08	18.70	7.63	
Scytonotus.....	73.42	62.22	37.25	55.21	57.83	2.66	5.28	4.78	5.88	2.60	9.05	4.01	2.83	0.36	
Deroceras.....	42.13	25.24	6.17	7.36	32.05	42.13	10.01	5.38	7.10	3.54	11.70	7.68	1.57	0.69	
Lithobius.....	5.74	12.86	10.75	5.93	8.50	6.33	9.43	8.35	6.65	5.44	13.83	7.68	0.42	0.69	
Spiders.....	18.84	18.57	11.63	13.29	15.81	8.77	7.31	7.75	1.21	3.19	7.98	7.73	0.77	0.69	
Large carabids.....	12.32	17.96	3.78	12.07	10.47	24.53	7.97	7.36	1.07	6.15	11.19	11.40	0.51	1.01	
Small carabids.....	8.65	2.86	10.58	1.43	7.43	2.00	3.30	0.14	0.39	0.71	1.60	2.33	0.36	0.21	
Staphylinids.....	4.45	8.73	22.61	6.55	11.18	16.54	6.51	0.32	1.22	4.74	5.33	8.58	0.55	0.77	
Histerids.....	3.68	13.81	11.47	5.32	7.99	1.78	2.13	0.34	0.48	1.84	1.60	2.69	0.39	0.24	
Nitidulids.....	3.10	3.17	2.41	2.86	2.86	0.78	0.66	0.60	0.31	—	—	0.47	0.14	0.04	
Parcoblatta.....	0.26	26.83	9.30	4.92	7.99	136.63	59.87	38.97	29.01	52.57	63.83	67.29	0.39	6.04	
Gryllus.....	6.26	108.10	0.56	9.00	22.17	151.39	47.73	83.30	107.42	58.64	85.11	84.99	1.09	7.62	
Myodocheus.....	1.55	15.71	13.23	8.79	4.32	2.00	3.16	0.06	1.55	1.54	12.79	1.67	0.21	0.15	
Retinella.....	19.68	70.00	15.23	8.79	24.24	2.00	3.16	0.44	20.37	0.47	13.83	5.49	1.19	0.49	
Cucujids.....	0.32	2.63	1.12	3.68	1.28	—	—	—	—	—	—	—	0.06	—	
Coccinelids.....	0.19	0.16	8.26	6.96	3.60	—	0.29	—	0.31	0.24	—	0.18	0.18	0.02	
Curculionids.....	0.26	1.59	0.24	0.41	0.48	0.11	0.29	—	0.31	0.47	1.60	0.31	0.02	0.03	
Diptera.....	1.42	7.78	0.24	1.64	2.09	0.11	0.29	0.02	0.46	0.12	—	0.22	0.10	0.02	
Ants.....	965.94	1544.40	2300.40	497.95	1425.43	1059.38	955.41	433.62	519.44	711.33	996.28	809.52	69.86	72.61	
Wasp.....	—	—	—	0.20	0.03	—	0.37	0.04	0.31	—	—	0.20	0.01	0.02	
Meracantha larv.....	0.45	0.32	8.26	6.96	0.51	0.11	0.15	—	—	—	—	0.07	0.02	0.01	
Other larvae.....	11.36	14.44	7.46	24.95	12.28	3.22	11.04	0.18	5.72	5.72	—	7.03	0.60	0.63	
Amphibia.....	0.13	0.62	0.08	0.61	0.26	0.33	—	—	0.15	0.12	—	0.13	0.01	0.01	
Other verts.....	—	0.16	—	0.41	0.08	0.11	0.22	—	—	—	—	0.09	0.00	0.01	

such differential counts. The most surprising point illustrated is that the staphylinids were more abundant in the sod than under the boards although typical of both niches. On some occasions large carabids were about equally abundant in the two habitats. Predators apparently exhibit less habitat specificity than the other forms and may find their prey in several niches.

THE DISTRIBUTION OF THE CRYPTOZOIC ANIMALS IN SPACE

The total numbers of cryptozoa counted in this study have been tabulated in Table 4. However, many of these forms were distributed differentially with respect to experimental areas and especially with respect to the grazed and ungrazed portions of the woods. In Table 7 the totals are tabulated according to areas and, to compensate for differences in amount of observation, all of the data are reduced to a basis of mean number of animals per 100 boards inspected.

From Table 7 it is obvious that most of the forms were most abundant in the ungrazed portion of the woods. Because there are certain known differences between the various areas, these data also suggest some factors which may be operative in affecting the distributions of the animals. Some of the differences between areas may be reviewed as follows:

1. The amount of organic matter and the water-holding capacity of the soil was highest in the ungrazed portion of the woods with the exception of Area D which was in the grazed portion but placed on soil transplanted from the ungrazed region.

2. The grass was always short in Areas A, D, and X and grass was practically absent in Area H.

3. In the ungrazed locality Areas H and TP received the most shade and were in the densest vegetation while Area X received the most sunlight. In the grazed locality Area B was the most shaded.

4. Areas A and B contained some double-sized boards and the two miscellaneous categories included larger boards and some stations which were concrete blocks or metal plates. Among the miscellaneous boards in the grazed locality there were three which were porous and had been cut from decaying logs.

5. Area O was the driest and was exposed to grazing cattle during the study.

6. Area C was on poor soil which still showed the effects of burning off thistle beds some years previously.

Very few forms were most abundant in the grazed part of the woods. The difference with respect to the large carabids is of doubtful significance but the roaches, crickets, and the unidentified psammochorid wasp were definitely more abundant on the grazed land.

The "large carabids" may be a heterogeneous group containing some forms which preyed largely on roaches and hence tended to be found most in areas where the roaches were abundant.

The roaches showed a definite selection of areas containing larger boards, Areas A and B and the "miscellaneous grazed" boards leading in the numbers of *Parcoblatta* found. Short grass also appears to be a factor as Area A led the grazed region and Area X was the only one in the ungrazed part of the

woods to contain many roaches. From the humidity gradient experiments it seems likely that humidity conditions in the ungrazed woods were, in general above the optimum for *Parcoblatta*. This is supported by the fact that Area D, containing the transplanted soil, was the poorest of the grazed areas despite its short grass.

The factors affecting the distribution of crickets are more obscure. The distribution of *Gryllus* by areas did not correlate well with grass height, soil humidity, or board size. The most suggestive correlation was with increased sunlight, for the four areas which received the most shade were also poorest in crickets. Casual observation also suggests that bright sunlight may drive the crickets into shelter under boards whereas they may remain out in the grass in more shaded locations.

Some of the animals, particularly *Lithobius*, the staphylinids, culeulionids, ants, and vertebrates, seemed to occur indiscriminately in the grazed and ungrazed locations. For the ants and staphylinids this may be a result of combining dissimilar species, and vertebrates were too few in number for their observed distribution to have much meaning. The culeulionids encountered are primarily soil and humus forms and their occurrence under the boards was probably quite accidental. *Lithobius* probably really was independent of the grazing factor and capable of inhabiting the cryptozoic niche in this woods wherever a food supply was present.

The miscellaneous larvae, a very heterogeneous group, and the lygaeid bug *Mydochus* were influenced by the spongy boards in the miscellaneous group in the grazed locality and hence their abundance in this locality is exaggerated by the table.

The other animals were almost all more abundant in the ungrazed part of the woods. Coccinelids entered the cryptozoic niche to hibernate and seemed to select areas containing tall grass while the nitidulid beetle *Glischrochilus* is a forest margin form in summer which migrates into the woods to hibernate, apparently tending to stop where the vegetation is most dense. Spiders probably simply descended from the vegetation to the ground level in autumn and hence tended to be most abundant in areas located beneath much vegetation. The cucujid beetle *Telephanus* is a soil and humus form apparently confined to the ungrazed part of this woods. When it was found under boards it was usually under those with grass beneath them. Reasons for the large lead in the seasonally occurring diptera shown by Area X are not clear but may be related to the short grass and humid soil since Area D was the richest in the grazed part of the woods. The tenebrionid larva *Meracantha* was almost confined to the ungrazed areas. This is another soil and humus form which seems to have been most abundant in the tall grass areas.

Of the animals which were more abundant in the ungrazed region, the factors influencing *Seytonotus*, *Deroceras*, and the histrid *Aeletes* are obscure. For the diplopods and slugs the two leading areas, X

and H, seemed to have little in common to differentiate them from the other ungrazed areas. The snail *Retinella* was apparently associated with short grass and moist soil as Area X led the ungrazed areas and Area D led the grazed areas. The spongy miscellaneous boards were often rich in fungus growth and also in snails. Small carabids were more abundant in the ungrazed areas and were chiefly associated with the areas receiving most shade. The isopods are very sensitive to low humidity and probably for this reason were most abundant in the ungrazed areas while, in the grazed region, areas containing larger boards and tall grass had the advantage. Soil type can probably be eliminated as a factor because Area D was poor in isopods.

THE SEASONAL DISTRIBUTION OF THE CRYPTOZOA

The abundance of each species varied considerably with season of the year. In Figure 2 the mean number of animals per 100 boards inspected is plotted by months for several of the more abundant or conspicuous species encountered in the cryptozoic niche. The data refer to the year 1942. The seasonal picture was similar for the other seasons of the study but inspections were made less regularly and the data are, therefore, less extensive.

The most striking variation in the cryptozoic fauna in this region comes late in October and in early November when many of the typical members of the fauna have begun to decline in numbers through vertical migration or, as with the roaches, through horizontal migration to take up hibernacula in decaying logs or under bark. At the same time many forms which normally live in vegetation descend to the forest floor and animals from the forest margin and thinly vegetated parts of the woods migrate into denser portions to hibernate. This phenomenon has been well described by Weese (1924) as follows:

"The most striking phenomena of the entire period covered by the collections were the hibernating reaction of the autumn, including a migration from the forest margin and downward to the forest floor, and the migration in the opposite sense in the spring. The principal inciting factors of the former seemed to be the fall of temperature and the great daily range of temperature of the early autumnal period. The latter was likewise a response to the changing temperature conditions of the forest, supplemented, perhaps, by changing moisture and light conditions. The fact that many species react alike and at the same time to the same stimulus or combination of stimuli shows a great degree of similar adjustment to the climatic rhythm of the temperate savanna on the part of the characteristic insects of the region."

In this study the spring migration outward from the cryptozoic niche was gradual and not very conspicuous but in the autumn forms which were not cryptozoic in summer, such as *Mydochus* and *Telephanus*, suddenly appeared under the boards in fair abundance. Less abundant forms such as coccinelids

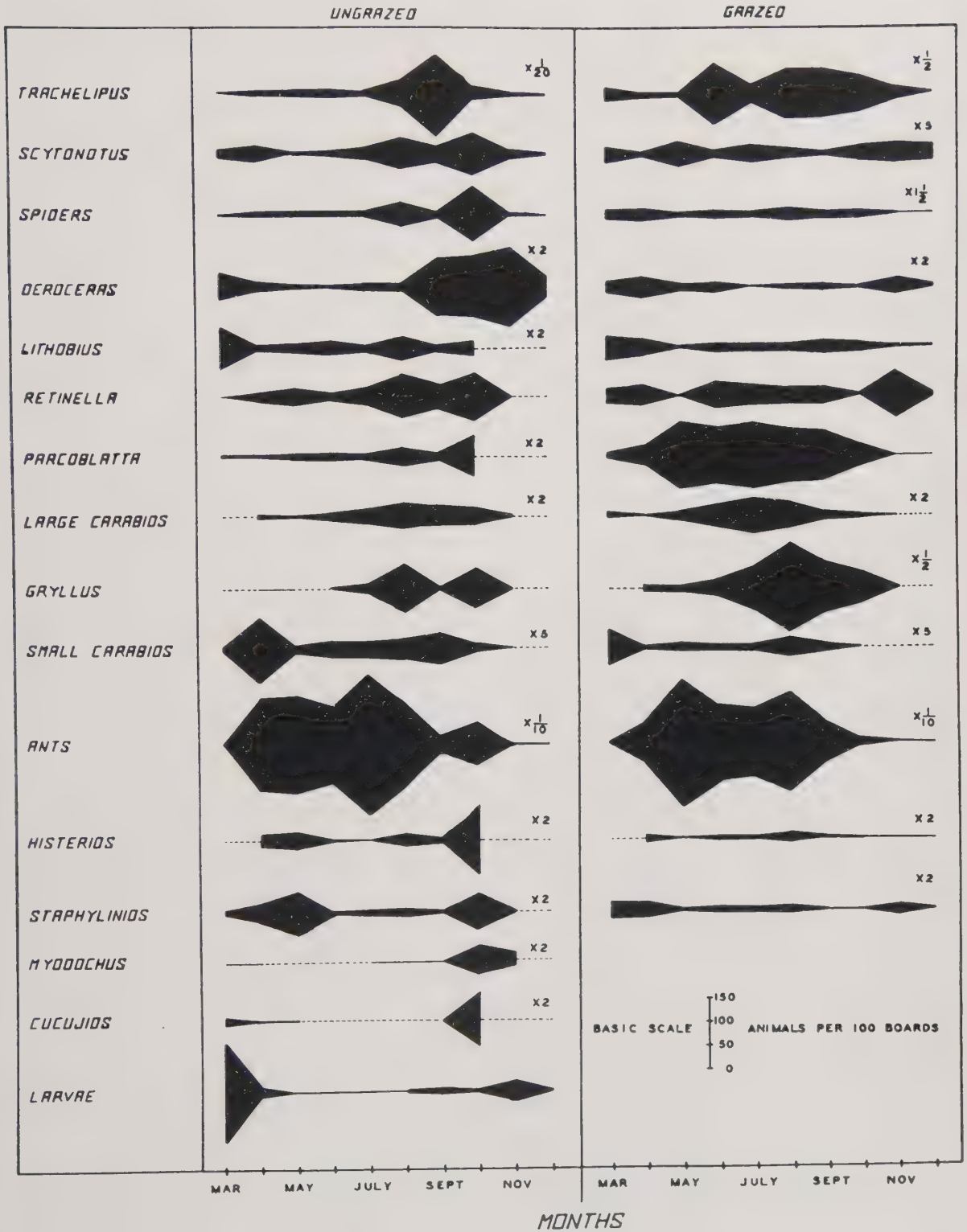


FIG. 2. Seasonal distribution of the cryptozoa.

and adult diptera which never appeared under the boards in June or July illustrate the same phenomenon. Other forms, the snails, slugs, and histerids, which were cryptozoic all year, showed an autumnal increase in numbers probably associated with the breeding season and the generally more humid conditions of autumn. At the same time other cryptozoa, best illustrated by *Parcoblatta*, showed a decrease under the boards in the grazed part of the woods and an increase in the ungrazed portion probably indicating a true migration into the denser part of the woods. Also at this time of the year there was a general decrease in the numbers of such typical cryptozoa as ants, carabids, centipedes, and isopods. Thus in late autumn and to a lesser extent in early spring the fauna of the cryptozoic niche varied considerably from the typical summer fauna composed largely of forms actually living and feeding in this niche.

In addition to the autumnal turnover in the fauna, Figure 2 shows an almost total disappearance of the cryptozoa in winter and, partly due to a very dry October in 1942, a general October decrease in all of the animals in the grazed portion of the woods. Other than these features it is noteworthy that the cryptozoic fauna showed little tendency to vary as a unit but that its composition at any particular time was the resultant of independent variations in abundance of the various species. The miscellaneous larvae, for obvious reasons, were very abundant in spring and reached a low level in mid-summer while the ants tended towards a mid-summer peak of abundance as did the isopods, large carabids, and crickets. The diplopods, spiders, and snails showed a fall maximum. The seasonal picture also varied between the grazed and ungrazed parts of the woods. Staphylinids in the grazed portion tended towards an autumn maximum while in the ungrazed region they showed two distinct maxima, in May and October. In the case of the carabids there was a tendency for the maximum to occur earlier in the grazed part of the woods.

Little evidence for any close integration between the various cryptozoic species was obtained. Weese (1924) recognizes six "seasonal societies" (prevernal, vernal, aestival, serotinal, autumnal, and hibernal) in each stratum of the forest and considers particular animals as typical of each seasonal society but the data of the present study provide very little reason for grouping the cryptozoa into seasonal societies. Certain forms were typically found in the cryptozoic niche and were, therefore, often found together, but altered conditions might largely or entirely exclude a portion of the fauna while leaving the remainder essentially unchanged. In the cryptozoic niche it seems sufficient to recognize a typical fauna which is present in the active season of the year and a vernal-autumnal faunal aspect when many forms not adjusted to life in this habitat enter the niche for purposes of breeding or hibernation.

In only two cases were the seasonal distributions of different species sufficiently parallel to suggest defi-

nite interrelations. The peak of abundance for large carabids showed some coincidence with the abundance of roaches and the graphs for spiders and diplopods show striking parallels. These cases will be discussed under biotic factors.

THE DISTRIBUTION OF THE CRYPTOZOIC ANIMALS WITHIN AREAS

It has been shown that different experimental areas representing slightly different habitats might contain faunas distinct from each other in species composition, seasonal aspects, and in relative abundance of various forms. Faunal variations within specific areas where conditions may be presumed to have been relatively constant may also be examined with respect to individual species to see to what extent individual animals were distributed at random in the available cryptozoic habitat.

A discontinuous integral variate such as the frequency of occurrence of a species of animal in field plots should be expected to correspond to a Poisson distribution (Poisson 1837, Student 1907, Svedberg 1922) if the individual animals are distributed at random. The application of the Poisson frequency distribution to cases where the number of samples is not very great or in cases such as would arise in field plot sampling of a fairly abundant species has sometimes been questioned (Whitaker 1914), but such applications have been vigorously defended by Arne Fisher (1922) and now seem to be generally accepted (Snedecor 1938, R. A. Fisher 1941). It is only profitable to investigate the distribution of the more abundant species because comparisons of observed and theoretical distributions are unsatisfactory for forms so rare that there is little probability of ever finding more than one individual under a particular board.

The distribution of spiders under the boards regularly corresponded to a Poisson distribution indicating a random distribution of individuals. Table 8 shows the distribution of 108 spiders encountered in 240 inspections of boards in Area H for the month of August, 1942.

TABLE 8. The distribution of spiders in Area H—August, 1942. $P = 0.527$.

	Number of spiders per board				
	0	1	2	3	More
Observed frequencies...	159	64	13	4	0
Expected (Poisson).....	157.0	66.5	14.2	2.0	0.3

The test of the observed distribution by the Chi-square test indicates that as great a deviation from the Poisson distribution could be expected about 53 percent of the time due to chance alone so there is certainly no reason for assuming a non-random distribution of the spiders under the experimental boards. In all experimental areas and at all seasons the spiders were distributed at random.

No other prominent species exhibited a random distribution of individuals. The chilopod *Lithobius*, which is generally considered to be a solitary animal, was never common enough under the boards to permit a rigid test of the randomness of distribution but, as already observed, they form winter aggregations which certainly indicates a non-random distribution for at least a part of the year.

All of the other important animals exhibited non-random distributions of the type termed "contagious" by Polya (1931). The distribution of 254 diplopods (*Seytonotus*) in Area H for a series of 360 inspections made between September 12 and September 22, 1942 will serve as an example of a contagious distribution. This distribution is shown in Table 9 and in Figure 3.

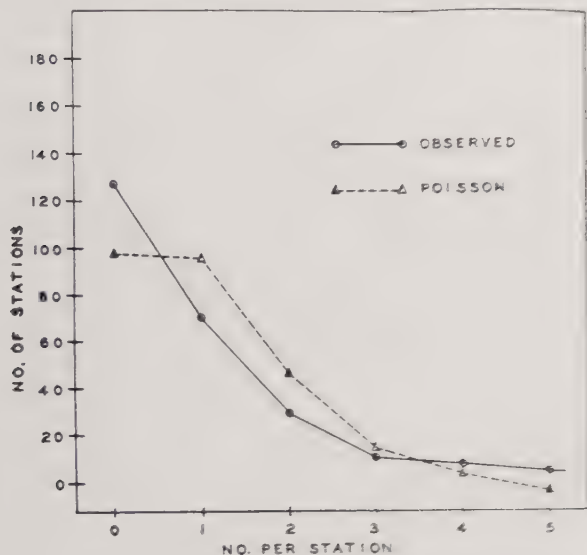


FIG. 3. The contagious distribution of *Seytonotus*.

Contagious distributions are characterized by a tendency for the animals to form aggregations so that the larger numbers of animals under single boards occurred more often than would be the case if the distribution were random.

TABLE 9. The distribution of *Seytonotus granulatus* in Area H. $P = 0.0000$.

	Number of <i>Seytonotus</i> per board						
	0	1	2	3	4	5	More
Observed frequencies	128	71	34	11	8	5	3
Expected (Poisson)	100.5	94.5	45.4	14.4	3.4	0.7	0.1

In testing randomness of distribution there is danger of confounding the results by lumping together data collected on different days or in different areas. For example, if data from the grazed part of the woods were included in the *Seytonotus* table, the form of the distribution would be radically altered because nearly all of these boards would show a

zero-frequency for diplopods. For this reason, interpretations based on such frequency distributions must be limited to the more common species and to as homogeneous samples as possible.

In the case of *Seytonotus* distributions were always contagious and showed a tendency to cross the theoretical Poisson distribution at about the level of the frequency class "3 diplopods per board." More detailed investigation might reveal that when about 3 *Seytonotus* are present under a board of this size they serve to attract other diplopods to the board or influence wandering individuals to remain once they find that particular board. Thus any "social instinct" on the part of the animals would lead to contagious distributions of the type observed.

In the case of the isopod *Trachelipus* the number of aggregations found usually did not exceed expectation until groups of 7 or 8 individuals were attained. Table 10 illustrates this for Area TP on June 12, 1942.

TABLE 10. Distribution of *Trachelipus rathkei* in Area TP—June 12, 1942.

	Number per board								
	0	1	2	3	4	5	6	7	8
Observed	25	25	14	11	8	11	2	3	3
Expected	5.7	17.5	26.8	27.3	24.9	12.8	6.5	2.8	1.1

	Number per board								
	0	1	2	3	4	5	6	7	8
Observed	1	1	1	1	1	1	1	1	1
Expected	1	1	1	1	1	1	1	1	1
Total expected over $k=0.5$	1	1	1	1	1	1	1	1	1

The isopods obviously tended to form larger aggregations than did the diplopods. The largest aggregation ever encountered under one board contained 56 isopods.

It is obvious that social insects such as the ants are not distributed at random but, aside from a social instinct, there are several other conditions which could cause animals to exhibit contagious frequency distributions. If an animal deposits its eggs in clumps, the newly hatched young will occur in groups and will be contagiously distributed. Neyman (1939), reasoning from this type of situation, has developed a class of theoretical frequency distributions which have been shown by Hall (1944) to give good fits when applied to certain contagiously distributed animals. Neyman's "type A" curve may be thought of as a generalized expression of the Poisson law with another parameter added. This type of distribution, however, seldom gave good fits in the present study where the basic assumptions were not realized. In highly contagious distributions such as those shown by the ants and isopods the fit was little better than that given by the Poisson distribution.

Another condition leading to contagious distributions is heterogeneity in the experimental areas. Unequal suitability of the boards for a particular species may cause the individuals to become aggregated under the boards with the more favorable habitat. This condition may be very difficult to detect because seemingly trivial factors might exert a great effect. It was found that boards over soil with a moisture content of less than 10 percent were definitely deficient in isopods so, at least at certain times, this factor would tend to produce a contagious distribution of isopods. The data on soil moisture are not sufficient for a detailed quantitative analysis of the effects of moisture on isopod distribution but part of the contagiousness of the observed distributions probably results from this factor.

Although soil moisture, and perhaps additional undetected factors, may lead to contagious distributions under the conditions of this study, it seems probable that a considerable part of the aggregating tendency observed is attributable to a mutual attraction between members of the same species. When mating is in progress paired animals are certain to occur more often than would be expected on an assumption of randomness. This is illustrated in Table 11 which shows the distribution of 60 small carabids in 500 inspections made during September, 1942.

Three of the seven observed pairs of small carabids were copulating when found and it is obvious that the frequency of pairs causes this distribution to depart from randomness.

In addition to mating, there are other advantages of associations between members of a species which could be operated upon by natural selection (Allee 1931, 1938) to accentuate aggregating tendencies. In the winter aggregations of centipedes, for example, no survival value is obvious but these aggre-

TABLE 11. The distribution of small carabid beetles—September, 1942.

	Number per board			
	0	1	2	More
Observed.....	447	46	7	0
Expected.....	443.4	53.2	3.2	0.2

gations are probably formed as a result of tendencies inherent within the individuals.

Whatever the cause of contagious distributions their occurrence considerably complicates statistical analysis of the data. Mean numbers of animals in different areas or time intervals cannot be compared by the usual methods employing standard errors because these methods assume random distribution of the populations. Also, the correlation coefficient cannot be used to measure association between species when the populations are not normally distributed. Consequently, it has been necessary to use presence or absence in samples as a criterion in making such comparisons.

The fact that nearly all of these species are contagiously distributed also makes it extremely hazardous to use sample collections in estimating any larger population. Even in a mildly contagious distribution this factor may be of considerable importance. For example, in an area of 20 boards such as Area H, 5 boards might be selected at random and the total population estimated by multiplying the observed number of animals by four. The results which could be obtained in this way can be calculated. As an example the distribution of 39 isopods in Area H on May 3, 1942 is shown in Table 12.

There are 15,504 different ways of drawing a sample of 5 boards from the 20 in this area and, by

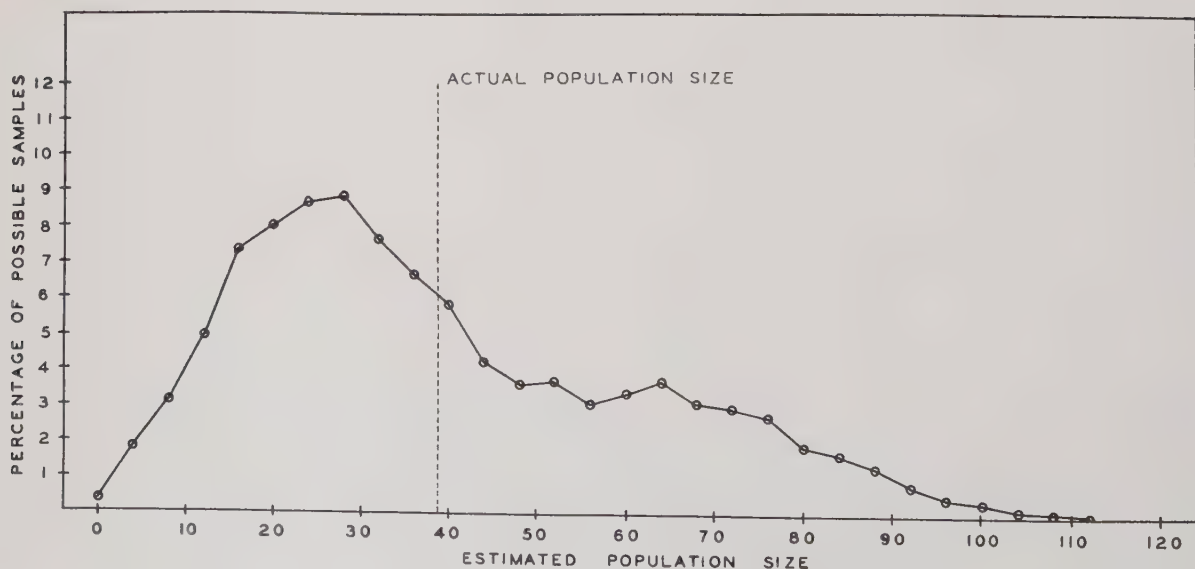


FIG. 4. Distribution of the possible samples for population estimation.

using such a sample to estimate the total isopod population of the 20 boards, 29 different estimates ranging from no isopods to 112 isopods could be obtained. The most frequent estimate of the total population would be 28 isopods and this value would be obtained 8.79 percent of the time. The distribution of the 15,504 possible samples is shown in Figure 4, and it illustrates that such a method of population estimation may lead to very great errors even when the distribution is not highly contagious. It is probably a general characteristic of contagious distributions that the population will tend to be underestimated from the mean of sample collections. This is to be expected because a disproportionately large percentage of the fauna is concentrated into a few units which are unlikely to be included in samples.

Because the observed contagiousness of these distributions seemed to result largely from a social instinct or attraction between individuals, it is very desirable to find some mathematical expression for the tendency to aggregate shown by a species at a particular time. This tendency is not constant but varies from day to day or even from hour to hour and also between experimental areas.

In a Poisson distribution the variance (σ^2) is equal to the mean (m) and the deviation of a frequency distribution from the Poisson distribution may, therefore, be expressed by the ratio: $\frac{m-\sigma^2}{m}$ or $\frac{\sigma^2}{m} - 1$. This expression will have the value 0 in a true Poisson distribution, will be positive when aggregation occurs, and negative when the animals are more evenly distributed (overdispersed) than would occur in the Poisson case. This expression is closely related to a number of others which have been employed such as the Lexis ratio (Arne Fisher 1922, Beall 1935), the second parameter in Neyman's "type A" contagious distribution (Neyman 1939), and the expression used by Svedberg (1922) and discussed by Gause (1936).

Attempts to use the above expression as a measure of aggregating tendency indicated that its value was greatly affected by the number of animals present, an effect also described by Arne Fisher (1922) and by Beall (1935). Since the formula for the variance

of a distribution may be written as: $\sigma^2 = \frac{\sum x^2 - m\sum x}{n}$

where x is the size of any sample and n is the number of samples, the expression: $\frac{\sigma^2}{m} - 1$ will

reduce to $\frac{\sum x^2}{\sum x} - m - 1$ in which form it is obvious that the ratio will tend to increase as the size of the samples increases. The Charlier coefficient of disturbance which may be written: $C = \frac{100\sqrt{\sigma^2 - m}}{m}$ is

independent of the number of animals and in the present study, as also found by Beall (1935), proved to be a much more satisfactory index of aggregating tendency. Positive values of C indicate aggregation while C becomes imaginary with overdispersion.

Imaginary values would be inconvenient for investigating animals if individuals showed actual antagonism toward each other but in this study all species were typically either underdispersed or randomly distributed so the occasional imaginary values of C were merely taken to indicate zero tendency to aggregate.

TABLE 12. Distribution of isopods in Area H—May 3, 1942.

Number per board.....	0	1	2	3	4	6	12
Observed frequency.....	8	4	2	3	1	1	1

A number of attempts were made to correlate values of C with physical or climatic conditions. Because many species tend to form autumn and winter aggregations one might expect to find values of C considerably influenced by low temperatures. Moisture conditions, in the laboratory at least, also influence the formation of aggregations by certain forms such as isopods.

For the period from September 16, 1942 to September 22, 1942 the boards in Area H were inspected every six hours. During this period there was an interval of hard rain and rapid temperature fall. These data then seem well suited for comparing variations in aggregating tendency and weather conditions. In Figure 5 the Charlier coefficient for isopods is plotted along with the air temperature taken some 30 cm. above the soil surface. This temperature was not necessarily the same as the micro-habitat temperature to which the animals were responding and the significant parallelism between the two lines is, therefore, all the more striking.

Another way of looking at aggregating tendency is to consider how the quantity $\sum x^2$ varies with the amount of aggregation. If aggregation is complete so that all of the animals are under a single board we will have: $\sum x^2 = (\sum x)^2$ while if the animals are distributed as evenly as possible so that there is zero aggregation we shall have approximately: $\sum x^2 = nm^2 = m\sum x$. Therefore, the increment representing amount of aggregation for any observed value of $\sum x^2$ is approximately $\sum x^2 - m\sum x$ and the maximum possible amount of aggregation is represented approximately by $(\sum x)^2 - m\sum x$. Expressed as a proportion, the observed degree of aggregation is then the ratio of the observed amount to the possible amount, or: $\frac{\sum x^2 - m\sum x}{(\sum x)^2 - m\sum x} = \left(\frac{n}{n-1}\right) \frac{\sum x^2}{(\sum x)^2} - \frac{1}{(n-1)}$ which is nearly equal to $\frac{\sum x^2}{(\sum x)^2}$.

At the time these data were being collected the writer made the then purely empirical observation that the quantity $\frac{\sum x^2}{(\sum x)^2}$ seemed to give a better representation of aggregating tendency as evidenced by significant correlations with air temperature than did the Charlier coefficient. This quantity was not used analytically because of its purely empirical nature

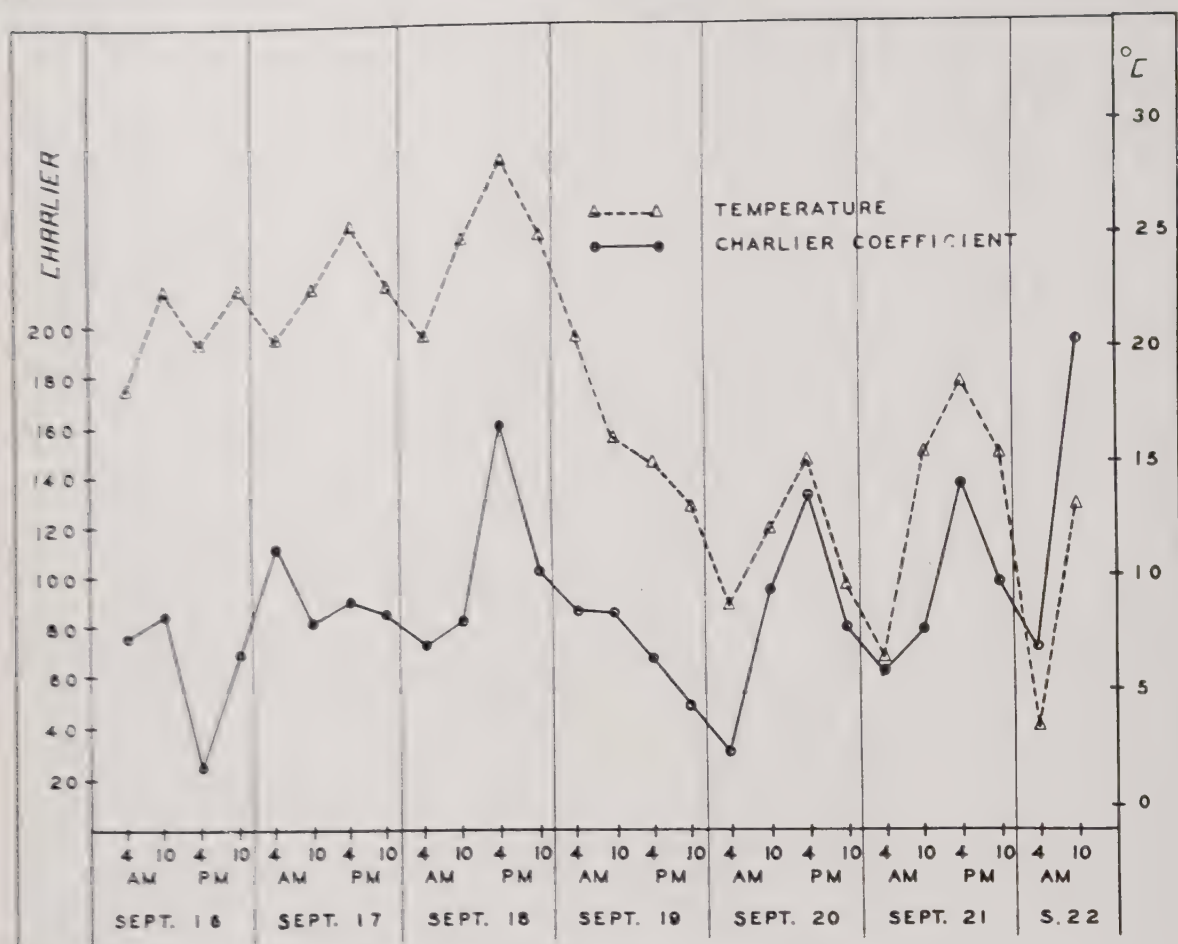


FIG. 5. Relation of isopod aggregating tendency to temperature.

and the lack of a rationale for ignoring the amount of aggregation, which would be expected to result from chance. It now appears, however, that some investigation might profitably be devoted to answering the question of whether it is the absolute degree of aggregation or the degree of excess aggregation which tends to vary with environmental factors.

The correlation coefficient between C and temperature was not significant, apparently because the downward trend in temperature was not accompanied by a general downward trend in the tendency of the isopods to aggregate, but the parallelism between the two lines may be tested for statistical significance by comparing the number of times the two lines rise or fall simultaneously. These data give the 4-fold table shown in Table 13.

TABLE 13. Significance test of the parallelism between temperature and C —the aggregativeness of the distribution of isopods. $P = 0.00017$.

	Increase in C	Decrease in C
Temperature increase	10	1
Temperature decrease	1	13

If C were independent of temperature we should expect to find the two increasing together only about 4.8 times instead of the 10 times observed. The probability value as calculated by Fisher's "exact method" (R. A. Fisher 1941) shows that a parallelism as great as that observed should occur by chance only about 7 times in 100,000 observations. Thus it appears that increases in temperature did increase the tendency of isopods to form aggregations in the cryptozoic niche.

This effect of temperature on aggregation tendency must be independent of any effect on the total number of isopods present because C is independent of this factor. Increases in aggregation then were almost necessarily brought about by isopods leaving slightly occupied boards and moving under boards where more isopods were present. There are evidently two ways in which weather conditions might effect this change. Either some inherent social tendency within the isopods must have been altered, or, as temperature changed, some boards must have become less favorable as habitats so that isopods left them. In this case there was no evidence of heterogeneity in Area H as evidenced by certain boards being consistently more occupied than others. Fur-

thermore, in the entire study, whenever heterogeneity was demonstrable in any experimental area, it tended to disappear when the soil became wet. Figure 5 shows a closer parallel between temperature and isopod aggregation in the period following the rain (the rain stopped at noon September 20) when the area should show less heterogeneity than in the earlier days. Thus the evidence favors the conclusion that some social tendency inherent within the isopods was increased by rising temperature. This is certainly not the only factor affecting the isopod aggregations or a much closer correlation should have been obtained but the temperature effect was highly significant.

This complicated behavior of the isopods, leaving shelter and moving to boards harboring larger numbers of isopods, as well as the vertical migration from unfavorable conditions, suggests that the complexity of aggregation phenomena has been underestimated in attempts to reduce these phenomena of mechanical responses such as altered rates of turning (Waloff 1941).

Any relationship between weather and aggregating tendency in other species was much less clear than for isopods. In Figure 6 the Charlier coefficient for

the diplopod *Scytonotus* is plotted for the same period shown in Figure 5. A comparison with the isopod graph makes it clear that the factors affecting the aggregating tendency of diplopods differed from those affecting the isopods. It is interesting to note the common tendency of the diplopods under the boards to be unaggregated (imaginary values of C) at the time of the 4 A.M. inspection which parallels the observation that *Scytonotus* may come out at night to aggregate on top of the boards or to wander in the grass. The early morning frost on September 20 may have been responsible for keeping the diplopods aggregated under the boards and at other times low atmospheric humidity might operate in this way. We do not at present, however, have sufficient data to correlate the aggregating tendency of *Scytonotus* with external conditions.

No species except *Trachelipus* and *Scytonotus* were common enough in this series of data to permit a satisfactory analysis of aggregating tendency. The Charlier coefficient becomes erratic when the mean number of animals per sample is very small and it would also be impossible to detect heterogeneity within the area from such limited data. Larger samples would be necessary to obtain satisfactory results with most of the other species.

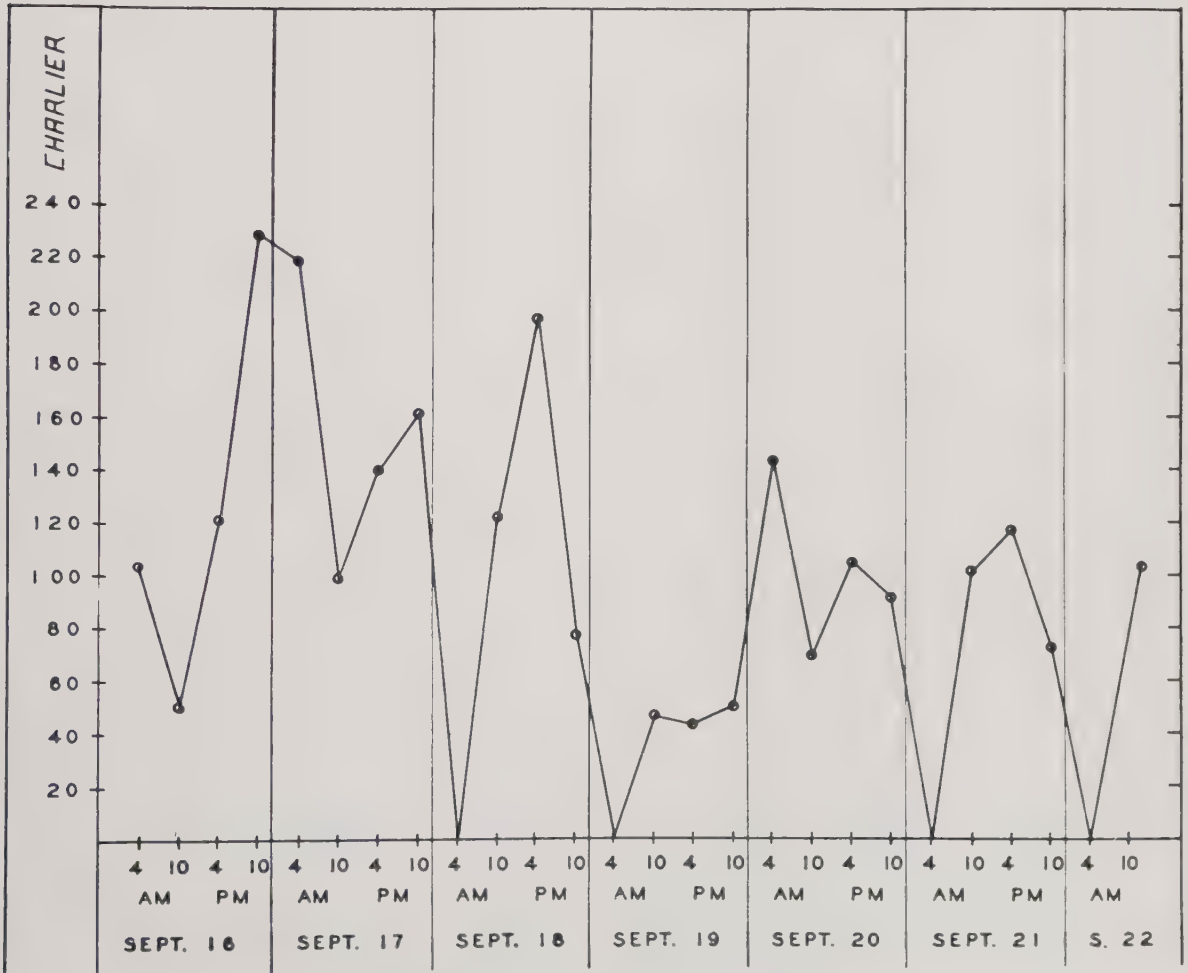


FIG. 6. Tendency of *Scytonotus* to aggregate.

BIOTIC FACTORS IN THE CRYPTOZOIC HABITAT

It has been pointed out that the vast majority of the cryptozoic animals feed upon general organic matter or are predators upon these omnivores. Thus relationships between living plants and the cryptozoa are indirect and of secondary importance. A cryptozoic fauna containing many of the essential features of the one here considered can thrive in the sandy soils of arid Turkestan or in the central desert of Iceland. Although Bornebusch (1930) found some differences between the soil and litter faunas in different types of forests, the essentially cosmopolitan nature of the cryptozoic fauna indicates that its members have no essential interrelations with particular species of plants. It is, of course, necessary to reserve judgment concerning the interrelations between the cryptozoa and microscopic plants, species of bacteria and fungi which may also be cosmopolitan in distribution.

Intraspecific relationships within the cryptozoic fauna have already been considered to some extent. Such relationships may take the form of antagonism between individuals, for example, cannibalism, or of mutual attraction between individuals ranging from association between copulating individuals to highly integrated social colonies as represented by the ants. The spiders were the only forms exhibiting no intraspecific attraction and here, too, if all individuals had been determined to species, it is likely that some relationships between individuals would have been evident. Centipedes, although definitely cannibals, form hibernating aggregations in winter and all of the other animals encountered exhibited to some extent a tendency to form aggregations. In every case there is probably some survival value connected with the possession of social or intrasocial tendencies but such values are not always easily detected empirically or experimentally (Allee 1931, 1938).

Interspecific relationships may take a number of types and, in the cryptozoic fauna which presents so many similar features in widely separated parts of the earth, one might expect to find many examples of close interrelations between various animal groups. When the same families and often the same genera and species are characteristically associated in the same habitat it would seem likely that a considerable degree of mutual adjustment and integration between forms might be present.

A critical search for examples of integration among the cryptozoa reveals surprisingly few interrelationships which may be considered as essential although local interdependencies between forms have been observed. Certain indirect relationships appear to be of some importance. Vertical migration of isopods to escape cold and drought usually takes place through holes dug by earthworms although holes left by plant roots or made by other burrowing animals are also used. It seems certain that in the absence of earthworms the isopod population would have been reduced due to the lack of avenues of es-

cape from lethal conditions. However, in the Brodskys' work on the soil fauna in Turkestan, earthworms were entirely absent but isopods were still an important part of the fauna. In this case the carabids which also tend to follow earthworm burrows were found to follow holes made by cecidionid larvae. Dammerman's studies include a number of islands totally without coleoptera but otherwise with typical cryptozoic faunas. A study of interrelationships between species in the present study then may help to clarify the position of this type of fauna with respect to ordinary concepts of ecological associations.

Forbes (1907, 1915, see Shelford 1915) was one of the early workers to attempt a quantitative study of the degree of association between species. He states (1915):

"To recognize, analyze, and locate an association with precision, use is made of the obvious fact that a biological association is composed of species which are more frequently associated with each other than they are with other species, and hence that frequency of *joint occurrence* of species in collections is a clue to their associate relationship. A certain chance frequency of joint occurrence will, however, result from an *indiscriminate* distribution of two species over the same area, although there may be no similarity of ecological relationship to bring them together; and this element of chance frequency must be eliminated before their frequency of ecological association can be distinguished."

The data relative to samples containing two species to be tested for association may be arranged in the form of a 4-fold contingency table as shown in Table 14.

TABLE 14. Arrangement of the 4-fold table for testing association between species.

Number of collections	Number of collections containing species B	Number of collections lacking species B	
Number of collections containing species A . . .	a	b	
Number of collections lacking species A	c	d	
Total number of collections	..	..	n

Forbes' "coefficient of ecological association" then may be expressed as: $\frac{na}{(a+b)(a+c)}$. This coefficient will have value of unity when the distribution of the species is random with respect to each other, will be greater than one when the species are positively associated, and less than one when they are negatively associated. Forbes' coefficient has the great disadvantage of being independent of the number of collections made so that there is no way of telling from its value when it is to be considered as statistically significant. This objection applies also to the

coefficients of Michael (1920) and Hacker (Calvert 1922).

The significance of the association between two species can be determined by calculating Chi-square (X^2) from the 4-fold table. With the table arranged as above: $X^2 = \frac{(ad-bc)^2}{(a+b)(c+d)(a+c)(b+d)} \cdot n$. When the values in the table are small, significance may be more accurately calculated by Fisher's "exact method" (R. A. Fisher, 1941).

From such a table it is possible to compute a number of coefficients of association which avoid the difficulties inherent in Forbes' coefficient (Yule and Kendall 1940, Pearson 1914) but the use of any such coefficient may be objectionable when it is known that the animals are not randomly distributed. Analysis has, therefore, been limited to testing the 4-fold tables for significant association between species without attempting to assign any value to the magnitude of such association.

TABLE 15. Association between *Deroceras* and *Trachelipus* in the ungrazed locality—June and July, 1942. $P = 0.0306$.

	Number of stations with:				Total stations
	Trachelipus only	Deroceras only	Both	Neither	
Observed . . .	365	3	38	100	506
Calculated . .	370.35	8.35	32.65	94.65	506.00

For the 16 groups of animals which were found in some numbers, 120 different pairs could be selected and tested for association. Most of these calculations would, however, be meaningless. It is obvious that there is no essential relationship between, for example, the roach *Parcoblatta* and the snail *Retinella* since one occurs almost exclusively in the ungrazed portion of the woods and the other almost entirely in the grazed locality. Similarly, adult "small carabids" showed an entirely different seasonal distribution from the slug *Deroceras*, reaching their peak of abundance at a time when slugs were very rare in the cryptozoic niche. It is certain that no mutual adjustment existed between these forms as would occur if the carabids depended upon the slugs for a food supply. Accordingly, tests for association have been limited to cases where some mutual adjustment might reasonably be expected. Such adjustments might be of either of the following types:

1. Two forms might be positively or negatively associated through responses to environmental factors. If, for example, both species tended to select boards where much moisture was present a positive association would be found while differences in reaction to moisture could result in negative association.

2. One species might be dependent upon another for a food supply or for in some way conditioning

the habitat. For example, isopods might be associated with burrowing forms simply because burrows provide avenues for vertical migration. In the case of a predator-prey relationship it is not clear whether one should expect to find a positive or a negative association between the species. A predator would tend to be attracted to boards harboring the prey species but the activities of the predator would tend to lead to an absence of the prey species. In any case it should be of interest to examine associations between predators and possible prey. Buckle (1923), using Forbes' coefficient, found a positive association between the carabid *Pterosticus* and elaterid larvae on which *Pterosticus* is known to be predaceous.

The occasionally significantly positive association between the slug *Deroceras* and the isopod *Trachelipus* may be used as an example of an association apparently due entirely to physical conditions. If the joint occurrence of these two forms is examined for the ungrazed part of the woods in June and July, 1942 the results shown in Table 15 are obtained.

The test of this distribution by means of Chi-square shows that such a chance positive association between the species would be expected only about 31 times in 1,000 trials, a result meeting usual conventional criteria of statistical significance. However, the joint occurrence data for these species in September of the same year (1942) yielded an entirely different result which is shown in Table 16.

TABLE 16. Association between *Deroceras* and *Trachelipus* in the ungrazed locality—September, 1942. $P = 0.9680$.

	Number of stations with:				Total stations
	Trachelipus only	Deroceras only	Both	Neither	
Observed . . .	227	47	189	57	520
Calculated . .	227.20	47.20	188.80	56.80	520.00

Table 16 suggests that the association between the two species is entirely a matter of chance. The difference between the two tables probably reflects moisture conditions. In hot, dry weather of mid-summer, significant associations were frequently found between forms sensitive to dryness such as *Trachelipus*, *Retinella*, *Deroceras*, and *Seytonotus* while in wet weather these forms were always distributed at random with respect to each other. This simply reveals heterogeneity among the boards. In dry weather the soil under some boards remained more moist than that under others and these species tended to remain in the more humid conditions.

A similar confounding of results may be obtained by lumping together various experimental areas when testing association. By combining data from areas in the grazed portion of the woods with data from those of the ungrazed locality one could usually

demonstrate positive associations between forms such as the isopods, slugs, and snails. A good example is furnished by the association between isopods and snails in the results of 465 inspections made in August and September, 1943 and shown in Table 17.

TABLE 17. Association between *Retinella* and *Trachelipus*.

	Total P = 0.0000		Grazed P = 0.0001		Ungrazed P = 0.2053	
	Observed	Calculated	Observed	Calculated	Observed	Calculated
<i>Trachelipus</i> only.....	221	236.65	145	153.45	76	79.46
<i>Retinella</i> only.....	13	28.65	1	9.45	12	15.46
Both.....	59	43.35	20	11.55	39	35.54
Neither.....	172	156.35	134	125.55	38	34.54

Table 17 shows a significant positive association between isopods and snails for the data as a whole and for the grazed portion of the woods but in the ungrazed portion an association as frequent as that observed would be expected about 21 percent of the time due to chance alone. Undoubtedly both isopods and snails occurred most under the boards where the soil was most humid. In the grazed locality certain boards were selected by both species leading to a positive association while in the ungrazed locality most (or all) of the boards provided suitable conditions and the species showed no special tendency to be found together.

A similar situation arose when boards of different sizes were considered together. Table 18 shows the association between *Trachelipus* and the roach *Parcoblatta* in Areas A and B for September, 1942.

TABLE 18. Association between *Trachelipus* and *Parcoblatta* in Areas A and B.

	Total P = 0.0216		Large boards P = 0.0001		Small boards P = 0.2020	
	Observed	Calculated	Observed	Calculated	Observed	Calculated
<i>Trachelipus</i> only.....	130	142.41	14	24.23	116	110.6
<i>Parcoblatta</i> only.....	86	98.41	26	36.23	60	54.6
Both.....	115	102.59	74	63.77	41	46.4
Neither.....	149	136.59	24	13.77	125	130.4

The two species were significantly associated if the data are considered as a whole but this association is seen to be due entirely to the fact that both species occurred most frequently under the large boards. Under the small boards the species were actually found together less often than predicted although this difference is not significant.

These examples show that great caution must be exercised in postulating essential relationships between species on the basis of evidence that they occur together more often than would be expected due to chance alone. Such associations can often, as in the

above examples, be shown to result entirely from similar reactions to some environmental factor. The apparent association between isopods and roaches shown above is obviously spurious as a biotic relationship because roaches were absent from the niches where isopods were most abundant and isopods were relatively rare in the areas dominated by the roaches. Thus environmental heterogeneity in the area sampled for joint occurrence may lead to apparent associations between species which are actually independent of each other. In certain cases we may identify the factor to which both species were responding but there is always the possibility that the species were responding alike to some condition which was undetected. Joint occurrence studies may provide significant evidence in support of direct evidence of biotic interrelationships but taken by themselves they may lead to entirely false conclusions regarding animal associations.

TABLE 19. Association between *Parcoblatta* and "large carabids"—August and September, 1942.
P = 0.0300

	Number of stations with:				Total stations
	<i>Parcoblatta</i> only	Large carabids only	Both	Neither	
Observed.....	101	32	20	312	465
Calculated.....	107.47	38.47	13.53	13.53	465.00

It was stated earlier that the large carabids feed to some extent on immature roaches, that these carabids and the roaches reached peaks of abundance at about the same time, and that both tended to be associated more with the grazed than with the ungrazed portion of the woods. This then is a case where we might logically expect to find association between two species. Table 19 shows the association between *Parcoblatta* and the large carabids for the 465 inspections made in August and September, 1943.

These data show a slight but significant association between the two forms, a result possibly attributable to the fact that neither was common in the ungrazed part of the woods. To test this possibility, the data from Area B only have been considered for 10 days selected at various times when both species were present. (1942: April 22, May 3 and 31, June 7, 12, and 28, July 4, 12, 23, and 30, and August 13.) These data yield Table 20.

TABLE 20. Association of *Parcoblatta* and "large carabids" in Area B for days when both species were present. P = 0.6274.

	Number of stations with:				Total stations
	<i>Parcoblatta</i> only	Large carabids only	Both	Neither	
Observed.....	117	28	22	173	340
Calculated.....	118.56	29.56	20.44	171.44	340.00

An association between large carabids and roaches as great as that shown in Table 20 would be expected due to chance about 63 percent of the time so it seems that our evidence fails to support a characteristic predator-prey relationship between these two forms.

TABLE 21. Association of *Scytonotus* and spiders—April and May, 1942. $P = 0.0051$.

	Number of stations with:				Total stations
	Spiders only	Scytonotus only	Both	Neither	
Observed.....	6	93	9	255	363
Calculated.....	10.78	97.78	4.22	250.22	363.00

The relationship between spiders and the diplopod *Scytonotus* differed somewhat from the roach-carabid relationship. Although we lack direct evidence that spiders feed on *Scytonotus* the seasonal (Fig. 2) and local distributions of the two exhibited considerable coincidence and for certain periods, particularly in the spring, these forms did exhibit significant positive association. This is illustrated in Table 21 for Area TP employing data of April 12 and 22 and May 3, 1942.

Later in the season when the spiders were more abundant they usually were not significantly associated with *Scytonotus* as shown in Table 22 which represents the data from Areas H and N for September, 1943.

TABLE 22. Association of *Scytonotus* and spiders—September, 1942. $P = 0.0892$.

	Number of stations with:				Total stations
	Spiders only	Scytonotus only	Both	Neither	
Observed.....	19	41	23	62	145
Calculated.....	23.46	45.46	18.54	57.54	145.00

Probably the association between spiders and *Scytonotus*, wherever it existed, resulted from similar responses to environmental conditions. It is possible, however, that certain spiders do typically feed on these diplopods and that this association has been obscured by combining data on these forms with data on other spiders.

PHYSICAL FACTORS

Evidence already presented indicates that animals in the cryptozoic niche are influenced by weather conditions and by physical factors such as soil moisture. Certain forms such as snails and isopods were shown to be associated with each other at times when the cryptozoic habitat was generally dry but not under humid conditions and the tendency of isopods to form aggregations was shown to be influenced by temperature changes. The mere fact

that each species shows seasonal fluctuations in abundance suggests that weather must exert an important influence. On a shorter time scale, considerable daily variations occurred in the numbers of individuals of each species found under the boards. That these variations were not purely random is shown by the fact that the numbers of animals in different experimental areas often fluctuated simultaneously. In Figure 7 the variations in numbers of isopods with time are plotted for Areas X and H for the same September, 1942 period discussed in connection with aggregating tendency. By comparing this graph for Area H with Figure 5 it may be noted that aggregating tendency did not correlate with the numbers of animals present and also that a considerable parallelism existed between the numbers of isopods present in Areas H and X during this period. The probability that this parallelism was due to chance may be tested as before in a 4-fold contingency table (Table 23).

TABLE 23. Significance test of the tendency for the isopod counts to vary simultaneously in Areas H and X. $P = 0.0244$.

	Increase in number of isopods in Area X	Decrease in number of isopods in Area X
Increase in number of isopods in Area H...	7	2
Decrease in number of isopods in Area H...	1	7

The test of Table 23 by means of Fisher's exact method shows that such a result due to chance would be expected only about 24 times out of 1,000. We may, therefore, conclude that some external factors were causing the isopods to enter or leave the cryptozoic niche. It may be noted that time of day and (by comparison with Figure 5) air temperature do not seem to have been important in this connection. The factors which were actually important in this case have not been identified.

It will be necessary to measure microclimatic factors actually within the cryptozoic niche to a much greater extent than was done in this study before it will be generally possible to recognize associations between fluctuations in the cryptozoic fauna and particular ecological factors. In a few cases it has been possible confidently to identify the physical factors which were affecting the fauna. Differences associated with contrasting experimental areas and seasons of the year have already been discussed but some of the differences between boards within single areas also led to faunal differences.

In Area X five of the boards were painted white, five were painted black, and five retained their natural wood color. On sunny days the temperature under the white boards was below that under the other boards and in dry weather certain faunal differences were ascribable to the surface colors of

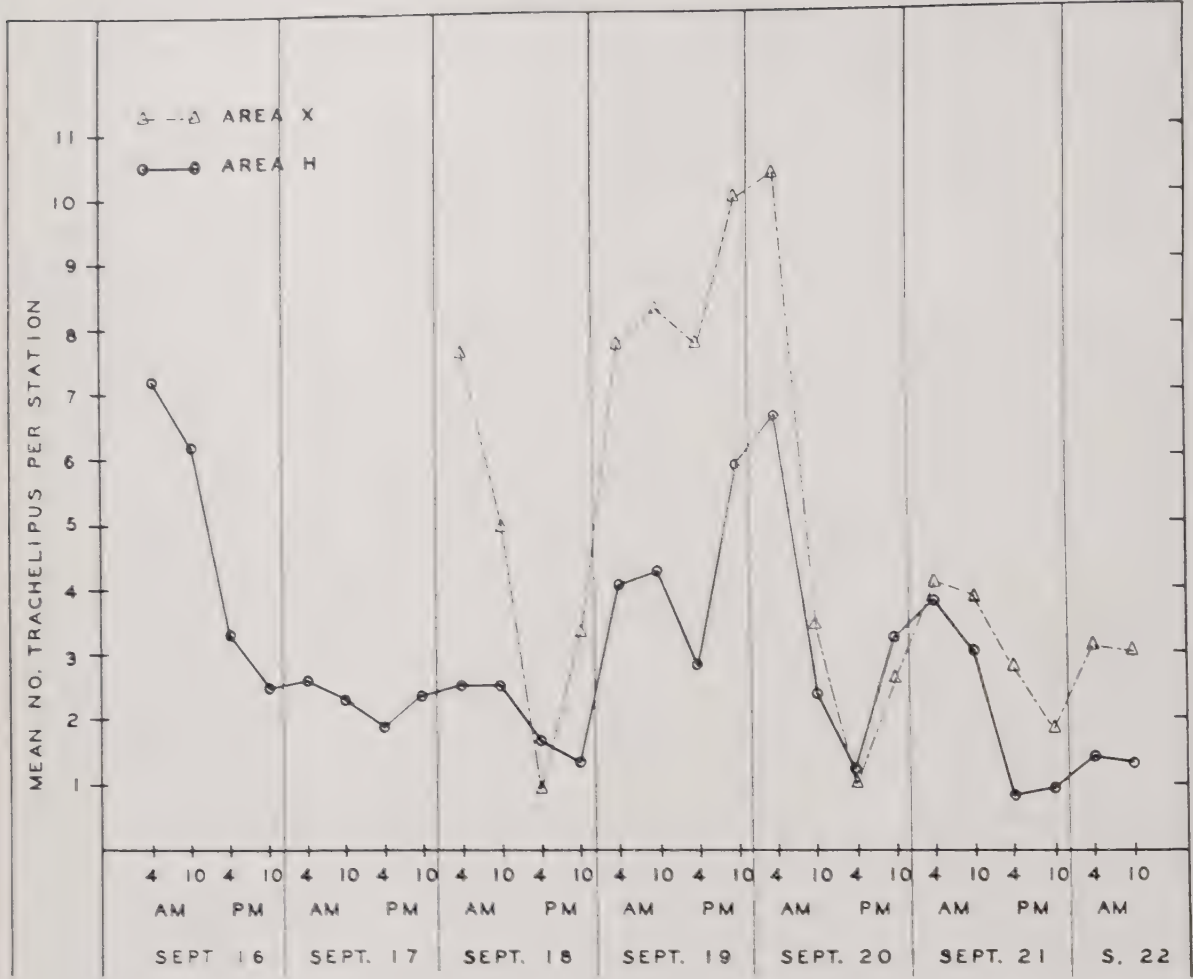


FIG. 7. Numbers of isopods in Areas X and H.—September, 1942.

the boards. Isopods, slugs, snails, and diplopods showed a tendency to be found least under the black boards and most under the white boards while the largest ant colonies seemed to occur under the black boards. Owing to the small number of boards involved, none of these differences was even statistically significant except in the case of the snail *Retinella*. In hot dry weather the snails tended to be found only under the white boards as shown for July 19, 1942 in Table 24.

TABLE 24. Distribution of *Retinella* in Area X with respect to the colors of the boards. $P = 0.0073$.

	<i>Retinella</i> present	<i>Retinella</i> absent
White boards.....	4	1
Not white.....	0	10

This association of the snails with the white boards was typical of the dry summer weather and was twice checked by changing the arrangement of the boards within the area. In each case the snails were

still associated with the white boards. This difference, however, disappeared entirely following rains or when the boards were watered with a sprinkling can even though the temperature differential remained. A temperature difference between boards, at least within the limits encountered in this study, seems not to affect the fauna directly but to exert an influence through more rapid drying of the soil under the warmer boards.

Further evidence for the importance of soil moisture in hot weather was obtained through daily watering of every second board in Area H for the week of July 19 to July 26, 1942. On July 26 it was found that the isopods and spiders tended to be concentrated under boards which had been watered. These results are shown in Table 25.

The effect of the watering on the spiders, while suggestive, was not statistically significant but the isopods were definitely associated with the more moist soil. Three attempts to repeat this experiment were ruined by the intervention of natural rain.

TABLE 25. The effect of watering on the distribution of isopods and spiders.

	Watered boards	Dry boards	P
Isopods present...	9	3	0.0198
Isopods absent...	1	7	
Spiders present...	4	0	0.0867
Spiders absent....	6	10	

On August 1, August 21, and September 26, 1943 a total of 311 soil samples was collected for analysis of soil moisture content and comparison with the faunal distribution. Of the samples, 166 showed a moisture content of over 10 percent of the 40° C. dry weight with a maximum of 29.3 percent while the other 145 samples showed less than 10 percent moisture with the minimum value being 3.3 percent. Table 26 shows how various groups of animals were distributed with respect to this arbitrarily chosen level of soil moisture.

TABLE 26. Distribution of the animals with respect to soil moisture.

Animal form	Proportion of boards occupied				Probability (from χ^2) that result is due to chance P
	Over 10% H ₂ O		Under 10% H ₂ O		
	Prop.	%	Prop.	%	
Parcoblatta (grazed woods)					
only.....	27/82	32.93	40/87	45.98	0.1198
Parcoblatta (total).....	33/166	19.88	41/145	28.28	0.0872
Trachelipus.....	125/166	75.30	67/145	46.21	0.0000*
Retinella.....	32/166	19.27	6/145	4.14	0.0001*
Scytonotus.....	49/166	29.52	30/145	20.69	0.0759
Gryllus.....	35/166	21.08	53/145	36.55	0.0024*
Gryllus (grazed woods)					
only.....	25/82	30.49	51/87	58.62	0.0025*
Histerids (Aeletes).....	24/166	14.46	9/145	6.21	0.0181*
Collembola (5 or more clinging to board).....	47/151	31.13	38/144	26.21	0.3682
Staphylinids.....	23/166	13.86	13/145	8.97	0.1772
Spiders.....	46/166	27.71	30/145	20.69	0.1574
Carabids.....	21/166	12.65	15/145	10.34	0.5222
Lithobius.....	17/166	10.24	8/145	5.52	0.1322
Deroceras.....	25/166	15.06	9/145	6.21	0.0132*

Table 26 reveals some interesting points. *Parcoblatta* and *Gryllus* were the only forms which seemed to select the drier boards and this was significant only in the case of *Gryllus*. The forms (with the exception of the collembola) which seemed not to discriminate at all between wet and dry boards were all predators—staphylinids, spiders, carabids, and *Lithobius*. This correlates with the suggestion made earlier that predators tend to range between the cryptozoic and other habitats and not to be restricted by the same conditions which affect the other cryptozoa. It was very surprising to find the collembola independent of soil moisture and this result must be attributed to the inadequacies of the sampling method for these forms.

TABLE 27. Association of isopod presence with absolute levels of soil moisture.

	MOISTURE RANGES					
	5-10 percent P 0.0001		10-15 percent		15-20 percent P 0.4010	
	Pro- portion	Per- cent	Pro- portion	Per- cent	Pro- portion	Per- cent
Boards occupied by <i>Trachelipus</i> ...	58/122	47.54	50/64	78.12	51/71	71.83

All of the other forms were more abundant under the boards where the soil was moist although results were significant only for the snails, slugs, isopods, and histerids. The marked association with moist soil in the case of the isopods has led to an attempt (Table 27) to determine quantitatively how dry a soil would be avoided by *Trachelipus*. Three ranges of moisture content have been selected for this comparison.

The boards with 10 to 15 percent soil moisture were definitely selected by isopods over the drier boards while a further increase in moisture seemed to produce no further effect. This discovery reflects back on the earlier discussion of the contagious distribution of isopods. In analyzing aggregating tendency we should omit from consideration any boards over soil with a moisture content of less than 10 percent. Probably no such dry soil occurred under boards in the September period for which aggregating tendency was analyzed (Fig. 5) but in dry weather soil moisture data would be essential for a critical analysis of this type.

Isopods not only tended to avoid the drier boards but there was also a tendency for them to form larger aggregations as the soil became more moist. In Figure 8 the mean number of isopods per occupied board has been plotted against soil moisture along with a trend line obtained by the method of averages (Lipka 1918). These data exhibit great variability due probably to the small number of determinations but they suggest that soil moisture may be another factor influencing the size of *Trachelipus* aggregations.

Areas A and B contained some boards which were twice the size of the standard boards and these large boards were especially rich in certain species of animals. This factor of board size may best be analyzed for Area B where every fifth board was of double size because here there was no possibility that the large boards might have been especially favorably located.

If animals found the boards by wandering about at random and stopping when they happened to encounter a board, larger boards would be expected to acquire more animals as a result of their greater periphery. The chance of an animal finding a board by random movements will tend to be proportional to the periphery of the board (Jackson 1939) which for each large board was 121 cm. and for each small

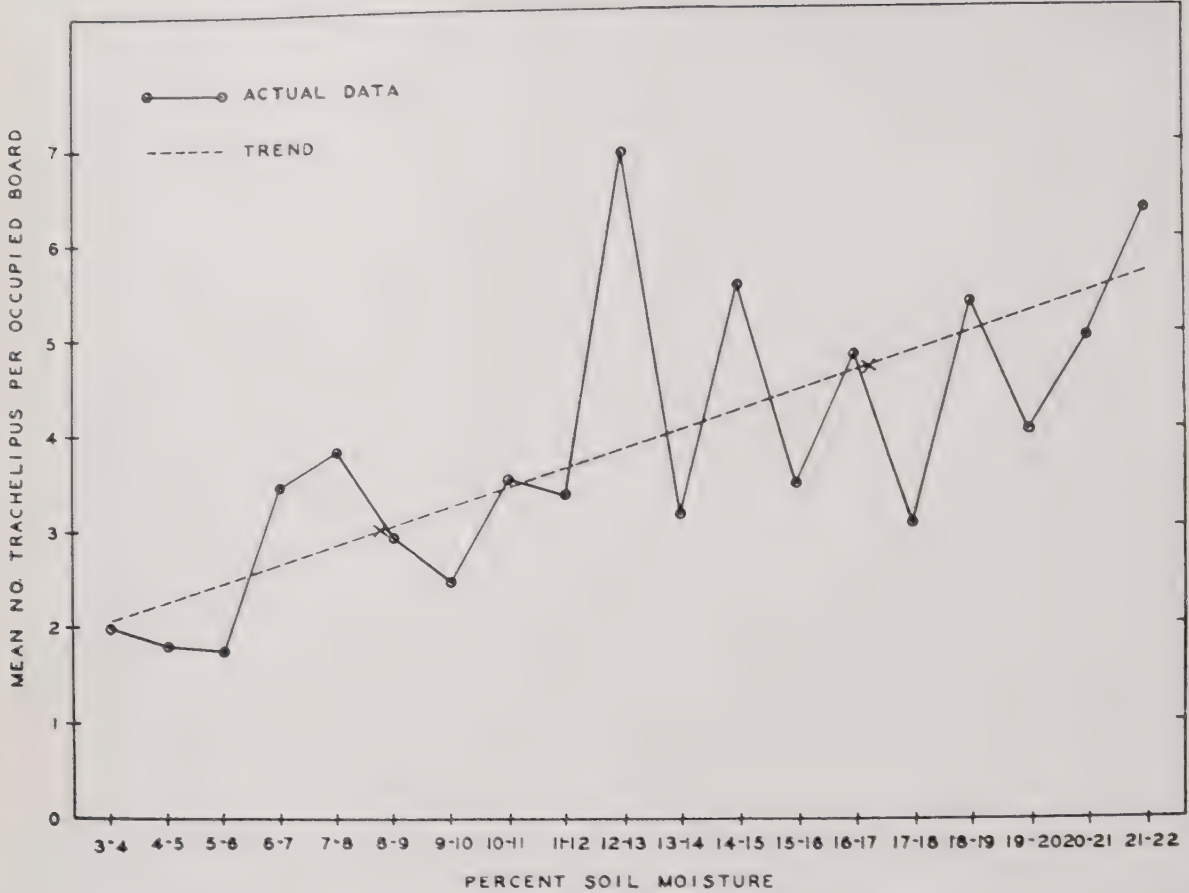


FIG. 8. Relation of the mean number of *Trachelipus* per occupied board to soil moisture.

board was 93 cm. The eight large boards in Area B thus had a total periphery of 968 cm, while the 32 small boards had a total periphery of 2976 cm. Thus, to compare large and small boards correcting for the effect of periphery, counts from the large boards have been multiplied by a factor of:

$$\frac{2976}{968} = 3.074.$$

Taking the results from 10 days of observation in the summer of 1942 and correcting the data from the large boards to compensate for periphery we obtain Table 28. In this P is determined from the binomial test described by Cole (1945) and gives the probability, if the large and small boards were equally likely to be occupied, that boards of either size would lead as often as (or oftener than) observed.

From Table 28 it appears that some special characteristic of the large boards repelled the ants and large earabids and attracted the roaches. Although the relative advantage of the large boards was greatly reduced in wet weather, soil moisture does not seem to be the factor which influenced the roaches because they were at all times significantly associated with large boards. We have no evidence by which we can identify the factor in operation here.

With respect to soil moisture the large boards provided a more constant environment than the small boards. In Table 29 the soil moisture under the 18 large boards in Areas A and B is compared with that under the nearest 18 small boards on August 21, 1943.

TABLE 28. The differential distribution of various animals with board size.

	Trachelipus	Lithobius	Spiders	Large Carabids	Small Carabids	Parcoblatta	Gryllus	Ants
Total number from 320 small boards...	904	74	34	10	28	258	366	9488
Total number from 80 large boards...	494	30	24	42	5	436	254	1821
Large-board total corrected for periphery.	1522	92	74	129	25	1343	782	5609
Ratio: Corrected large:								
Small	1.67	1.24	2.18	12.90	0.89	5.21	2.18	0.59
Proportion of these 10 days when the corrected large board counts exceeded the small boards	7/10	6/10	6/10	1/8	3/4	10/10	5/7	1/10
P from binomial	0.344	0.754	0.754	0.070	0.625	0.002	0.453	0.021

TABLE 29. Comparison of soil moisture under large and small boards.

	Mean % soil moisture and S. E.	Coefficient of variation (C. V.) and S. E. P < 0.01
Large boards.....	7.53±0.17	9.37±1.56%
Small boards.....	7.25±0.37	21.39±3.56%

Although the mean percentage of soil moisture was about the same under large and small boards, the large boards were significantly less variable in this respect.

DISCUSSION

Objects such as logs and stones lying on the soil surface provide beneath them an available animal habitat with certain unique characteristics. The microclimate in this niche is characterized by constantly high humidity as contrasted with outside conditions, by relative absence of air movement and illumination, and by temperature conditions more stable than in the open. Fungi may grow in this niche and provide a food supply for certain animals but other plant life is essentially absent. Roots of growing plants, commonly present in the general soil habitat, are largely absent from the cryptozoic niche.

The vast majority of terrestrial animals must, for at least a part of their lives, escape exposure to light and to dry air. Buckle (1923) estimates that 95 percent of all insects pass some period of their life history in the soil and other groups of animals such as nematodes, crustacea, and molluscs are typically even less tolerant of dryness than are the insects. Thus, with respect to physical conditions, the cryptozoic niche provides a habitat suitable for a vast variety of animals. The majority of such animals, however, are capable of burrowing in the soil and thus of utilizing a habitat which is much more extensive than the cryptozoic habitat. Such forms, the earthworms and pseudoscorpions are good examples, may be found in the cryptozoic niche simply because conditions there are suitably dark and humid. To these forms the habitat beneath a board is merely a small portion of a habitat of considerable vertical and horizontal extent. The situation is different for forms which are poorly adapted for burrowing. Such forms find in the cryptozoic niche shelter conditions similar to those within the soil and also, because the burrows of the true soil fauna may enter the cryptozoic niche, avenues along which non-burrowers may migrate into the subterranean stratum to escape extremes of environmental conditions. The inability of these forms to penetrate solid wood largely excludes them from the physically similar habitat in the interior of fallen logs although this shelter may become available to the cryptozoa after logs have been penetrated by other animals. Animals within logs also cannot readily migrate to depths sufficient to

provide escape from extremes of environmental conditions such as the extreme subcortical temperatures which may be attained by logs exposed to the sun (Graham 1920, Craighead 1920). Although many cryptozoic animals can and do hibernate in decayed logs, such forms as the isopod *Trachelipus* which cannot tolerate freezing may be excluded from this habitat by winter temperatures in a region such as that considered in this study.

The cryptozoic niche then lacks the potential food supply of living plant material which is exploited by many species in the hypogeous fauna. Forms such as isopods, certain diplopods, and collembola which can utilize the general organic matter of the soil are better able to reside in the cryptozoic niche than are subterranean forms such as many eurypterid and scarabeid beetles which feed largely on plant roots. For similar reasons many wood-eating forms characteristic of the fauna of fallen timber are excluded from residence in the cryptozoic niche. The specific requirements of the forms which are poor burrowers but require shelter cause them to become concentrated in the cryptozoic habitat and competition for available space may be a factor in excluding from this habitat forms which are also capable of living in other niches. In the present study well over 80 percent of the cryptozoic animals were very omnivorous forms. A few forms, mycetophilid larvae and the snail *Retinella*, utilize as food the fungi growing in the cryptozoic niche and a few others, such as the slug *Deroceras* and some of the ants, merely find shelter in this niche and forage for food in other habitats when environmental conditions permit.

The terrestrial cavernicolous fauna is also composed largely of non-burrowing and euryphagous forms but they are distinguished from the cryptozoa primarily by their greater morphological modifications. Its typical members exhibit some modifications in pigmentation and in sense organs which distinguish them from related forms living outside of caves (Racovitza 1907). This fauna also parallels the cryptozoic fauna in its lack of integration because its members are recruited from diverse groups and apparently have in common only the ability to avoid competition and unfavorable environmental conditions on the outside. As with the hypogeous fauna, but for different reasons, no absolutely sharp line can be drawn between the cavernicolous fauna and the cryptozoic fauna.

Associated with the characteristic omnivores in the cryptozoic habitat are predators which, as is usual in any fauna (Elton 1935), are much less abundant than the key-industry forms. As has been shown quantitatively, the predators are not especially confined to the cryptozoic habitat but also prey on the fauna of the mineral soil and of other niches. The predators in this niche are much the same all over the world because they are the characteristic predators of the soil habitat, a formation of world-wide distribution and, at least on a temporal basis, nearly world-wide continuity.

The cosmopolitan constancy of the typical cryp-

tozoic fauna of omnivores reflects the fact that these forms are adapted to, and largely restricted to, a habitat which is of very general occurrence but which locally is always quite limited in extent. In these local niches the characteristic cryptozoa thrive and far outnumber the less restricted members of the hypogeous fauna which can avoid competition with the cryptozoa by moving a short distance horizontally or vertically. The cryptozoa may also spread vertically in cases where the soil has been loosened and mixed thus providing better aeration and distributing organic matter to greater depths. Thompson (1924) found that the fauna descended more deeply on arable land which had been plowed and Motter's 1898 study of the grave fauna revealed many forms present at unusual depths.

If we allow for replacements by closely related species, we have in the cryptozoic fauna a series of forms comprising an association of fairly constant composition over much of the earth. Considering the broad aspects of this fauna we find it functioning as a part of various widely different larger biotic assemblages. The constancy of this fauna whether found on deserts, tropical islands, grasslands, or in various types of woodlands has already been stressed. Yet when we turn to the minute examination of the cryptozoa within a single 40-acre oak-hickory forest we find a surprising absence of essential interrelationships between species. Nor is the situation clarified if we follow Forbes in making use of "the obvious fact that a biological association is composed of species which are more frequently associated with each other than they are with other species." We would by this criterion find a *Trachelipus-Parcoblatta* association if we concentrated our examination on large-sized boards on recently grazed land with short grass during dry periods in mid-summer but, by moving a few meters to collect in an area with tall grass, we would conclude that these two species avoid each other. Several parallel examples have been given. The conspicuous members of this fauna apparently have, as Jacot (1940) stated, been brought together by the influence of many different conditions and the precise composition of the fauna is only maintained under a precise combination of values of various factors.

The evidence that the cryptozoic fauna, like hot-spring faunas and the fauna of human dwellings, is held together primarily by common habitat requirements and tolerances of the constituent species suggests a qualitative distinction from such highly integrated animal communities as, for example, the willow-gall community described by Walsh (1864). In the writer's opinion, it would be a mistake to apply the same name, "biocenosis" or "animal community," to the two types of species assemblages. In the absence of positive evidence of interspecific organization it seems safest, and most conserving of the community concept, to refer to the cryptozoa as a fauna. The attempt of Harshberger (1911) to force the soil fauna into a sort of supraorganismic

concept has been rejected by Clements & Shelford (1939) and both Buckle (1921) and Jacot (1940) have commented on the apparent lack of biotic interrelations within the soil and litter faunas.

SUMMARY

1. The cryptozoic fauna is the fauna of small terrestrial animals which normally live beneath stones and logs and in similar habitats. Except in spring and autumn this fauna is quite distinct from the true soil fauna and other related assemblages of animals. Its primary distinction seems to lie in the fact that most of the species inhabiting this niche are very omnivorous and are consequently independent of living vegetation. Most of the characteristic cryptozoic animals are also sensitive to drying and to exposure and are poorly adapted for digging.

2. Associated with the cryptozoic omnivores is a series of predators less restricted to this niche. These predators also prey on the fauna of the mineral soil.

3. The cryptozoic faunas of all regions for which information is available are strikingly similar.

4. Boards placed on the forest floor acquired a typical cryptozoic fauna which was studied quantitatively. The most prominent groups of animals were the pulmonate gastropods, one species of terrestrial isopod, spiders, centipedes, diplopods, collembola, crickets, roaches, beetles, and ants. The particular species encountered tend to show close affinities with those which inhabit this niche in other regions.

5. The majority of the cryptozoic species reached their maximum abundance in the portion of the woods which had longest been protected from grazing by cattle and some evidence suggests that this was largely an association with relatively humid soil. A few animals, notably the orthopterans, were more abundant in the drier grazed portion of the woods. Some species were found to be associated with specific and very local conditions such as height of grass.

6. The cryptozoic fauna as a whole tended to reach a maximum in terms of abundance in the wet weather of early autumn although some species were exceptions. The faunal picture changed radically in late autumn when many of the characteristic species left the cryptozoic niche through vertical or horizontal migration and many species typical of other niches moved under the boards to hibernate or oviposit.

7. The spiders were the only animals to show a random distribution of individuals under the boards. All of the other forms abundant enough for analysis exhibited contagious distributions showing a tendency to form aggregations. This aggregating tendency in many cases appears to result from tendencies inherent within the individual animals. Statistical studies of this fauna are complicated by the occurrence of these non-random distributions. A statistic, the Charlier coefficient of disturbance, was found to be satisfactory as an index of intensity of the aggregation tendency and, in the case of the

isopods, values of the Charlier coefficient were found to be significantly affected by changes in air temperature. It is suggested that more observations of this type may prove useful in animal census studies at least to aid the investigator in determining the most favorable time to conduct a census.

8. No constant or essential interspecific relationships were detected in the cryptozoic fauna. In all cases where species were significantly associated with each other the apparent association could be shown to be due to sample heterogeneity. There is great danger of confounding the effects of sample heterogeneity with biotic interrelationships whenever joint-occurrence data are used in defining an animal association.

9. It is shown that weather conditions influence the numbers of animals found in the cryptozoic habitat but the specific meteorological factors have been identified in only a few instances. Of the factors investigated, soil moisture conditions exerted the greatest effect on the fauna.

10. The cryptozoic fauna can be best understood when considered as an assemblage of animals brought together by similar responses to, or similar tolerations for, conditions of the physical environment. Interspecific integration among the cryptozoa is very inferior to that found in other species assemblages which have been referred to as animal communities or biocenoses and the writer has, accordingly, avoided such terminology.

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